The wintering and migration ecology of the whinchat *Saxicola rubetra,* a declining Palearctic migrant

by
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Submitted for the degree of Doctor of Philosophy
to the University of St Andrews

December 2014

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ABSTRACT

For migrant birds, the non-breeding season can greatly influence survival and future reproductive success. Knowledge of annual and overwinter survival, the degree of site fidelity and habitat use in the non-breeding season, migration ecology, routes and stopovers, and whether these differ with age or sex is fundamental to understanding population dynamics, vulnerability to anthropogenic habitat degradation, and consequently for understanding the severe widespread declines of migrant bird species. The degree to which a migrant is a winter specialist or generalist is likely to be central to understanding population dynamics. I studied survival rates and the wintering and migration ecology of a declining Palearctic migrant, the whinchat *Saxicola rubetra*, wintering in West Africa, to establish how the non-breeding season may influence migrant population dynamics. Whinchats were extremely site faithful both within and between years, holding distinct winter territories and returning to those territories in subsequent winters, despite the opportunity to relocate. Overwinter survival was very high and annual survival was comparable to or higher than that reported on the breeding grounds. Because our power to detect resident and dispersing birds was high, survival rates likely estimated true survival well. Habitat characteristics varied widely across territories and territories were smaller if more perching shrubs and maize were present. Most individuals showed a tolerance or even preference for human modified habitats. Some individuals may have multiple wintering sites. There was no evidence of dominance-based habitat occupancy or any differences in winter ecology, site fidelity, survival and most aspects of migratory behaviour between age and sex classes. Migratory connectivity occurred only on a large-scale and individual migratory behaviour was also varied. Fundamentally, the results suggest a generalist strategy in the non-breeding season within their wintering habitat of open savannah, most likely as an adaptation to stochastic site selection within the wintering range for juveniles undertaking their first migration plus changing and unpredictable conditions both within and between years. Consequently, wintering conditions may not significantly limit whinchat populations and mortality is probably highest during

active migration. Notably, non-specialist migrants such as whinchats may have some resilience at the population-level to the increasing anthropogenic habitat modification occurring in Africa, suggesting that conditions during migration and in Europe may be driving declines; yet establishing the currently unknown thresholds of any resilience is likely to be fundamental for the future conservation of migrants.

ACKNOWLEDGEMENTS

Quite simply, this PhD would have been impossible without the support of many people, to which I owe a great deal of gratitude. My supervisor Will Cresswell went above and beyond his duties to give me the time, support, encouragement and enthusiasm I needed both in Africa and the UK, not forgetting some excellent Scotch after mid-season fieldwork. His support has helped me write a thesis that I am proud of. To everyone at APLORI who made my work possible: to Ulf for his kindness and encouragement, Arin and the field assistants for their hard work, Phil Hall, Chima, Azi, Ester, Joseph, Manu, Daniel 'Admin', and the other staff, students, and visiting lectures for their help, hard work and humour. My fellow student Sam gave me support and friendship throughout and made the first steps of the PhD so much easier. All of these people and others made Nigeria not just bearable but a fun, memorable place.

I couldn't have done this without my family or my partner Chris. My parents have always supported and encouraged me to do what I love, without question, and I wouldn't be anywhere remotely close to where I am now without them. Through our adventures in Africa – only possible because of her generosity – my sister Sara gave me a perfect introduction to this amazing continent that helped me to get through the frustrations and drawbacks with an open mind and a sense of humour. This proved to be invaluable from the word 'go'. I am indebted to Chris for the sacrifices he has made to enable me to do my PhD, and for his constant support and encouragement. Without him or my family this would have been immeasurably harder.

Finally, this work could not have been undertaken without the Leventis Conservation Foundation, Chris Goodwin, and the great generosity of Tasso Leventis who funded this PhD.

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CHAPTER 1. INTRODUCTION: ECOLOGY AND POPULATION DYNAMICS OF PALEARCTIC MIGRANTS DURING THE NON-BREEDING SEASON

This thesis will explore how events occurring outside of the breeding season may influence the population dynamics of Palearctic migrants that winter in Africa. Although migrants spend the majority of their lives away from the breeding grounds, our knowledge of their non-breeding ecology is limited and poorly reflects the influence that this period has on the populations of migrants. The dramatic declines seen in migrant populations across the World and our modest understanding of the drivers of these declines highlights the importance of understanding the role of the non-breeding season in shaping migrant populations.

1.1 What it means to be a migrant

Birds show huge diversity in their life-history strategies and the solutions they adopt for balancing the energetic constraints of growing to maturity, reproducing and surviving throughout the annual cycle (Bennet and Owens, 2002). Seasonality causes both temporal and spatial variation in resource and food availability, abiotic conditions, and predation, amongst others, requiring adaptations and flexibility to ensure survival and successful reproduction in both the short and long term (Newton, 2006a). If individuals are unable to compensate, seasonality demands range shifts in order to find the conditions and resources necessary to ensure both short and long-term survival (Newton, 2006a). Migration is one life-history strategy that enables individuals to maximise survival and reproduction in a seasonal and variable environment, and individuals may move huge distances in response to seasonal changes in food availability and to take advantage of transient resources for breeding and survival throughout the year (Hedenström, 1993). Of the migratory vertebrates, birds are the most diverse group of terrestrial migrants – over 80% of the breeding birds in North America are migratory (Morton, 1992; Rappole, 1995) – yet though being a migrant may enhance survival and reproduction across several

temporal scales, it demands a complex life cycle involving dividing the annual cycle into different stages, all of which may affect population dynamics.

1.2 Migrant declines: the role of the non-breeding season

In both the Palearctic and Neotropics, migrants are declining (Sodhi et al., 2011; Vickery et al., 2014), and these declines are occurring at faster rates than similar non-migratory species (Heldbjerg and Fox, 2008; reviewed by Vickery et al., 2014). This suggests that the trait of being a migrant itself may be making some species more susceptible to declines. Several mechanisms have been identified; but because migrants can be affected by conditions that occur in different geographical regions and at different times throughout their annual cycle, the specific causes of these declines are hard to pinpoint (Newton, 2004; Vickery et al., 2014). These causes are also likely to be species and population-specific. Although conditions during the breeding season have been implicated in the declines of many migratory species, (for example 78% of the Palearctic migrant species evaluated by Vickery *et al* (2014) are affected by human-related habitat change on the breeding grounds), the non-breeding period itself is frequently considered to be the most influential in limiting migrant bird populations (Marra et al., 1998; Sherry and Holmes, 1996). By showing that declines are related to migration distance and habitat type at wintering latitudes, Sanderson *et al* (2006) suggest that the wintering period is important in the decline of a significant number of Palearctic migrants. Winter population limitation has been identified previously for several Palearctic species such as common whitethroat *Sylvia communis*, sedge warbler *Acrocephalus schoenobaenus*, sand martin *Riparia riparia*, and barn swallow *Hirundo rustica* (Baillie and Peach, 1992), a pattern which is also mirrored in the Neotropics (Marra et al., 1998; Norris et al., 2004; Rappole and McDonald, 1994; Robbins et al., 1989; Sherry and Holmes, 1996). Such a strong influence on population dynamics is often suggested to be because migrants spend the majority of their annual cycle away from the breeding grounds, either migrating or wintering (Marra et al., 1998; Sherry and Holmes, 1996), which likely increases the number of factors that influence survival and population

dynamics. Determining which aspects of the non-breeding season limit migrant populations is therefore key to the conservation of migrants.

1.3 Survival during the non-breeding season: explaining large-scale declines

The non-breeding season is divided into two main stages: actively migrating and wintering, both of which can be broken down further into periods that influence survival. During migration to and from the wintering grounds, the migratory strategy and behaviours adopted, departure and arrival decisions, the migratory journey itself and how to fuel flight, stopover ecology, how to avoid predators, and when to moult, can all hugely influence survival. On the wintering grounds, winter habitat selection and the implications both habitat and predation have for body condition; seasonal habitat changes; competition; and the ability to locate suitable habitat, determine both survival and future reproduction. The decision to be itinerant or site faithful; individual age and sex-related effects; the degree of migratory connectivity and carry-over effects between migratory stages; plus the growing impact of climate change and other anthropogenic factors such as hunting, all have further implications for survival and population dynamics. Consequently, there are many strategies for maximising the benefits and lessening the costs of being a migrant.

1.3.1 Migration

The migratory journey itself magnifies many of the constraints already acting on individuals throughout their lifespan and introduces additional constraints and associated trade-offs. Fundamentally, active migration itself is costly, and often the main source of adult mortality (Newton, 2007), which can be 15 times higher during migration compared to stationary periods (Sillett and Holmes, 2002). Many decisions influence the success of migration and its implications for future survival and breeding success. The timing of departures and arrivals; whether to interrupt migration and stop for refuelling, and if so, where to stop and for how long; how fast to fly, at what times, and for how long; what route to take; how to respond to weather conditions and how to avoid predation during migration, can all have a

significant impact on survival and population dynamics (Newton, 2010a). Departure and arrival dates are well established to have a significant influence on future survival and reproductive success (Lozano et al., 1996). Survival during migration is strongly influenced by wind patterns and how these shape migratory routes and migration ecology (Chernetsov, 2012b; Erni et al., 2005). Wind speed can influence the timing of migration and arrival dates, and so reproduction upon reaching the breeding grounds and annual productivity (Drake et al., 2014). Weather during migration can directly cause mortality or can divert migrants from their chosen migratory routes (Newton, 2007). Where and when to stop during active migration to replenish fuel reserves are vital decisions for the success of migratory flight (Chernetsov, 2012b; Newton, 2010a); but the location and duration of staging sites are often governed by the location and width of ecological barriers (Chernetsov, 2012b; Rubolini et al., 2002). Further considerations such as predation risk and when to moult are also important for survival, and the degree of migratory connectivity has implications at the population level.

Migratory strategies

In avian migration, two main migratory strategies have been proposed. Initially, Moreau (1961, 1972) proposed that migration was undertaken by non-stop flights across barriers such as the Mediterranean sea and Sahara desert in a single journey lasting 40-60 hours (Bairlein, 1992). Observations of significantly fewer birds in deserts during daylight than estimated to be migrating, plus low densities of migrants at oases, supported this claim (Moreau, 1972; Moreau, 1961; Salewski and Schaub, 2007), and further observations of rapid fat store accumulation during autumn in the Mediterranean and during spring in the Sahel were seen as an adaptation for non-stop flight (e.g. Bibby and Green, 1981; Finlayson, 1981; Fry et al., 1970). Previously, little knowledge existed as to whether birds found at oases had stopped migrating or were “fall-outs” (Bairlein, 1985a), although theoretical investigations into the feasibility of non-stop flight suggested that observed fat stores could fulfil such energetic demands (e.g. Biebach, 1990; Moreau, 1972; Pennycuick, 1972; Tucker, 1974; Wood, 1982). In agreement, many species have

been found to undertake non-stop flights, especially shorebirds such as great knots *Calidris tenuirostris* (Pennycuick and Battley, 2003) and bar-tailed godwits *Limosa lapponica* (Gill Jr et al., 2005).

A more recent contrasting theory is that of intermittent migration, in which birds interrupt migration at stopover sites to rest and refuel before continuing to their destination (Bairlein, 1985a, 1992; Bairlein et al., 1983; Biebach et al., 1986). This is supported by more recent studies of migrants at desert locations along migration routes (e.g. Bairlein, 1992). Birds captured in the Mauritanian desert during spring migration have been found carrying high fat loads, and therefore could not be "fall-outs" due to energy deficit alone (Salewski et al., 2009). The authors estimated that 85% of birds could reach the desert edge through intermittent flight (Salewski et al., 2009). Observations of large numbers of migrants in good condition in seemingly hostile environments further supports the intermittent flight theory (Bairlein et al. 1983, Bairlein 1985, 1992, Biebach 1995). It is now established that the majority of small long-distance passerine migrants may stop over strategically at sites to replenish fat stores for onward flight (Bairlein, 1985a, 1992; Bairlein and Totzke, 1992; Biebach, 1985; Biebach et al., 1986; Erni et al., 2002a; Salewski and Schaub, 2007; Salewski et al., 2009; Schmaljohann et al., 2007; Yohannes et al., 2008). Nevertheless, it is important to point out that we can only effectively sample those birds that do stop migrating, for whatever reason, as an unknown proportion of migrants may be migrating overhead without stopping.

Migrants use various flight strategies during migration, incorporating non-stop and intermittent flights (both long and short), orientation along specific routes or borders, stopovers at specific sites, nocturnal flight, loop migration, and use of shade and oases, amongst others (for example see Bairlein, 1991; Bairlein, 1985a, 1992; Bairlein et al., 1983; Bairlein and Totzke, 1992; Biebach et al., 1986; Pearson and Lack, 1992; Schmaljohann et al., 2007). Because species and individuals have different requirements, migratory strategies vary greatly both between and within species regarding the distance and routes travelled, the timing of departures and arrivals to and from staging areas, the duration of journeys, and the location of

stopovers (Delingat et al., 2007; Newton, 2010a, b). All of these have implications for survival and population dynamics (Newton, 2010b). Some generalisations can be made, however. Most insectivorous passerines are nocturnal migrants, for example (Bolshakov et al., 2003; Martin and Busby, 1990).

Departure and arrival decisions

Reaching a destination quickly and efficiently is fundamental for both reducing the costs of migration and maximising survival and future reproduction, especially for long-distance migrants. Time constraints act throughout migration, and so when to begin preparing for departure is an important consideration. Departure times should coincide with favourable weather conditions to maximise survival during migration, and with high resource availability to optimise pre-migratory fattening and minimise the costs of acquiring and maintaining fat reserves (Delingat et al., 2007). The timing of arrival and departures is further driven by which stage follows in the annual cycle. Birds arriving earlier on the breeding grounds often have greater reproductive success because of the advantages early arrival has for mate choice and the ability to attract a mate (Potti and Montalvo, 1991); breeding territory establishment (Alerstam and Lindström, 1990); choice of available resources (Aebischer et al., 1996); body condition upon arrival (González-Prieto and Hobson, 2013; Sandberg and Moore, 1996); earlier pairing (Slagsvold and Lifjeld, 1988); and fundamentally the ability to fledge or recruit more offspring by breeding earlier and with repeat broods (Aebischer et al., 1996; Lozano et al., 1996; Møller, 1994; Verboven and Visser, 1998). Yet there are costs to early arrival (Kokko, 1999), such as reduced survival if weather is unseasonal (Newton, 2007).

The timing of arrival on the wintering grounds can be fundamental to winter survival. As with breeding, earlier arrival in winter may give individuals a competitive advantage when establishing a territory (Alerstam and Lindström, 1990). Late arrival has been linked with delayed moult in some migrants, and may negatively impact the return migration to the breeding grounds (Conklin and Battley, 2012). Delaying departure from the breeding grounds also puts birds at risk of early unseasonal

weather before departure (Newton, 2007). Such events can reduce local breeding densities by 30 – 70% (Newton, 2006b). Because of the links between arrival date and reproductive success, departure times from the wintering grounds are often more finely tuned. Spotted flycatchers *Muscicapa striata* show less variability in their departure dates from the wintering grounds than arrival from the breeding grounds, for example (Kok et al., 1991). Both experimental and field evidence has established that departure from the wintering grounds is controlled by circadian rhythm, as determined by photoperiod and day length (Gwinner, 1996; Kok et al., 1991).

Environmental conditions can strongly influence the timing of migration. Birds are more likely to depart when conditions are favourable, such as when tailwinds are present and winds speeds are low (Åkesson and Hedenström, 2000; Åkesson et al., 2002; Schaub et al., 2004). With the use of radio telemetry, Eurasian reed warblers *Acrocephalus scirpaceus* have been shown to depart when tail winds are present, correlate departure direction with wind direction, and also compensate for wind drift; behaviours which were more pronounced at higher wind speeds (Åkesson et al., 2002). Northern wheatears *Oenanthe oenanthe* also time their departure at stopovers with favourable wind conditions (Delingat et al., 2007), and have been shown to undertake nocturnal exploratory flights before departing, suggesting that migrants sample meteorological conditions before migrating (Schmaljohann et al., 2011). Departures of common whitethroats were unaffected by weather conditions in a study of departure from a coastal autumn stopover site, however (Fransson, 1998), and departure direction of northern wheatears has been shown to be unrelated to wind speed (Schmaljohann et al., 2011). This suggests that other cues are also important for departures. Most likely, some migrants may depart when environmental conditions will not *severely* affect migratory flight, and some may be forced to depart regardless of environmental conditions because of time constraints.

The migratory journey

Because active migratory flight is costly, the decision to migrate a long or short distance and choice of route can have profound implications for population

dynamics. Migrants should travel the shortest distance possible and should do so under favourable and predictable conditions if the costs and duration of migration are to be minimised. A single long-distance non-stop flight is often the most optimal way to reach the destination (Alerstam and Lindström, 1990), as some migrants such as great knots (Pennycuick and Battley, 2003), bar-tailed godwits *L. lapponica baueri* (Gill Jr et al., 2009), sharp-tailed sandpipers *Calidris acuminata* (Handel and Gill Jr, 2010) and ruddy turnstones *Arenaria interpres* (Thompson, 1974) demonstrate. But the feasibility of undertaking a single flight to the destination becomes constrained by distant staging areas and geographical barriers (Chernetsov et al., 2007; Delingat et al., 2007; Klaassen, 1996). Because flight distance is dependent upon fat load (Alerstam and Lindström, 1990), acquiring or carrying sufficient reserves may become inefficient or even impossible. Stopovers are then necessary to refuel and rest, which results in the intermittent flight pattern of many smaller migrants (Biebach et al., 1986; Klaassen, 1996; Salewski et al., 2009). Individuals are likely to favour short-distance flights between stopovers because this requires less energy, and so reduces the time needed to remain at stopovers to accumulate large reserves, plus exposure and vulnerability to predators when foraging due to impaired evasion from being heavier (Alerstam and Lindström, 1990; Fransson and Weber, 1997; Houston, 1998; Ydenberg et al., 2004). When to terminate migration is also fundamental, because reducing the distance between the breeding and wintering areas lowers the chance of mortality during migration from starvation and predation, reduces total migration time, removes the need to acquire and carry large fat deposits, and may eliminate the need to interrupt migration to rest and refuel entirely.

Consequently, migration routes, distances, and speeds can vary considerably both across species and within different populations. Radio-tracking of arctic terns *Sterna paradisaea* have revealed that some individuals undertake annual flights of over 80,000 km (Egevang et al., 2010). Some populations of bar-tailed godwits migrate 11,000 km non-stop from Siberia to western and northern Australia or from Alaska to New Zealand (Conklin and Battley, 2012; Gill Jr et al., 2005). Alpine swifts *Tachymarptis melba* undertake 200 day non-stop flights by foraging and roosting on

the wing (Liechti et al., 2013). Ringing recoveries have revealed that spotted flycatchers migrate 10,000 km between breeding and wintering areas (Kok et al., 1991). Red-backed shrikes *Lanius collurio* perform a loop migration of 22,000 km, travelling further during spring than autumn (Tøttrup et al., 2012), and migration distances of c. 14,500 km have been recorded for northern wheatears (Bairlein et al., 2012). European robins *Erithacus rubecula* range from being migratory in northern Europe to resident in the south, with intermediate populations in-between (Andriaensen and Dhondt, 1984; Arizaga et al., 2010). North American blue grouse *Dendragapus obscures* migrate less than 50 km (Cade and Hoffman, 1993; Herzog and Keppie, 1980). Such variation in migration strategies across species means that migration can take from as little as one day to over three months, equating to over half a year for some long-distance migrants (Newton, 2010b).

A further consideration is the differing time constraints between spring and autumn and the influence of environmental conditions (Newton, 2010a). Spring migration is often faster than autumn migration (Åkesson et al., 2012; Alerstam, 2003; Bächler et al., 2010; Fransson, 1995; Schmaljohann et al., 2012), most likely because of the greater pressure for prompt arrival on the breeding grounds (Newton, 2010b). Environmental conditions such as wind speed, wind direction, and weather can have a profound influence on migratory behaviour and the success of migration (Erni et al., 2005; Newton, 2007). Mortality can occur from storms and adverse weather, especially when birds are crossing barriers such as water or deserts and become exhausted or run out of fuel with no possibility of landing (reviewed in detail in Newton, 2007). The risks of migration have been suggested to be greater for smaller birds, and those travelling longer distances – especially over inhospitable terrain and when weather conditions are adverse (Newton, 2007) – because flight speeds are often related to wind patterns, speed and direction (Erni et al., 2005; Erni et al., 2002b; Piersma and van de Sant, 1992). Migrants can, however, compensate for wind drift during migration (Åkesson, 1993). For song thrushes *Turdus philomelos*, for example, the timing of arrival at the wintering grounds and passage in the Baltic region has been correlated with temperature, wind and precipitation (Sinelschikova et al., 2007). Mass nocturnal migration may then occur when conditions are most

favourable, such as when wind conditions aid flight (Bolshakov et al., 2003). Large-scale wind patterns – such as those over the Sahara – have a great influence in shaping migratory routes and flyways (Erni et al., 2005). The direction from which birds depart from stopovers is often correlated with wind direction (Åkesson and Hedenström, 2000), and the effect of weather is often related to body condition (Butler et al., 1997). Departure direction is related to fuel load on departure for northern wheatears, for example (Schmaljohann et al., 2011), where heavier birds are able to migrate along their chosen route, even when faced with an ecological barrier, but lean birds are forced to fly in alternative and most likely less optimal directions (Schmaljohann et al., 2011). Migrants have been shown to compensate for wind conditions en route (Åkesson et al., 2002), and strong winds or unfavourable wind patterns can result in detours during migration (Åkesson et al., 2012).

Fuelling migration

The need to build and replenish the substantial fat reserves to fuel the energetic demands of long distance flight is one of the most important considerations for migrants (Bauchinger et al., 2005; Klaassen, 1996; Pennycuick, 1989; Pennycuick, 1975; Woodrey and Moore, 1997). Distances may be crossed over barriers where fuelling is not possible, and adequate reserves must be acquired and stored if individuals are to reach their next available refuelling site (Delingat et al., 2007; Fransson et al., 2005). Fundamentally, the maximum width of any barrier that can be crossed is determined by the amount of fat and protein that can be deposited and used for fuel (Salewski et al., 2010). Many species double their body mass during periods of pre-migratory fattening and during stopovers, such as semipalmated sandpipers *Calidris pusilla*, eared grebes *Podiceps nigricollis*, blackpoll warblers *Setophaga striata* and several Palearctic migrants (e.g. Bauchinger et al., 2005; Blem, 1980; Fry et al., 1970; Jehl Jr, 1997; Klaassen, 1996; Lövei, 1989; Maillet and Weber, 2006; Nisbet et al., 1963; Odum et al., 1961). For garden warblers *Slyvia borin*, an increase in food intake, fat, protein and carbohydrate utilisation, and increased nutrient assimilation efficiency corresponds with times of pre-migratory fattening (Bairlein, 1985b). In a study exploring daily mass changes of 14 migratory species at

stopover sites in Canada, Dunn (2002) estimated that most migrants could accumulate sufficient reserves for migration in a minimum of 2 – 3 days. Some migratory species, however, complete migration with very little fat, such as Eurasian reed warblers (Bolshakov et al., 2003; Chernetsov, 1999). Time constraints act on migrants during periods of fattening, resulting in a trade-off between fuel accumulation rates and the duration of migration, its associated risks, and the impact of fat stores on the energetics of flight (Klaassen, 1996). Fattening should begin in time for sufficient resources to be stored for flight and to insure against unpredictable food availability, but not so soon that the costs of maintaining an increased mass are prolonged (Witter and Cuthill, 1993).

Fattening in birds does not simply reflect food availability. Compared to low weight periods during winter, higher energy utilisation suggests that body mass is related to a cycle of nutrient utilisation and not food intake alone (Bairlein, 1985b). A study on sedge warblers revealed that less than half of individuals will lay down large fat reserves when food is unlimited (Bayly, 2007). This suggests that factors other than food availability influence fuelling behaviour and the level of reserves accumulated before departure, for example spatial and temporal cues reflecting seasonal variations in resource availability (Bayly, 2007). A large consideration is that the need to store reserves for flight requires individuals to increase their mass above what is the optimum for balancing the trade-off between starvation and predation risk (reviewed by Lima, 1986).

Not knowing the exact migratory pathway or weather conditions en route, whether the next stopover will have adequate resources for refuelling, or the fattening rates at future sites, may also result in birds needing reserve levels that are higher than the optimum (Dierschke et al., 2005; Schaub and Jenni, 2001). This would be expected if the benefits of preparing for unpredictable situations outweigh the costs of carrying additional fat. The impact of wind conditions on flight speed changes with differing fat loads (Alerstam and Lindström, 1990; Delingat et al., 2007), adding further complexity to the decisions governing mass on departure from stopovers and demanding flexibility if migration and survival are to be optimised.

Barriers influence stopover ecology, and therefore how migration is fuelled, for several species (Lindström and Alerstam, 1986; Rubolini et al., 2002), most likely because of the demands of obtaining sufficient reserves. Barn swallows carry more reserves if a larger barrier must be crossed to reach the wintering grounds (Rubolini et al., 2002). Common chaffinches *Fringilla coelebs* migrating in Europe rest at stopovers to restore reserves when they are confronted by an ecological barrier (Lindström and Alerstam, 1986). Blyth's reed warblers *Acrocephalus dumetorum* have been found to carry more fat before desert crossings than other migrants faced with smaller barriers (Chernetsov et al., 2007). These studies highlight the importance of selecting sites at which to refuel, as enough fuel must be acquired to successfully cross any ensuing barrier (Schaub and Jenni, 2001). This also suggests that any additional reserves needed to cross barriers are acquired from staying longer at fuelling sites, or are accumulated along the migration route prior to reaching the barrier (Schaub and Jenni, 2000a, b). Yet a study of four passerine migrants at 14 stopovers along the migratory route found that the proximity of ecological barriers to stopover sites explained higher fattening rates for only one species (Schaub and Jenni, 2001), suggesting other factors influence fat reserves. A strategy of reverse migration, where migrants backtrack after encountering a barrier to locate suitable stopover sites, is another adaptation to barrier crossing (Delingat et al., 2007; Komenda-Zehnder et al., 2002).

Overall, because the constraints acting throughout migration – the distances and routes travelled; the location, number and duration of stopovers; and the environmental conditions faced – will differ according to the migratory strategy of a species and the body condition of individuals, the amount of reserves migrants needed for optimal migration will vary considerably across species, populations and individuals.

Stopovers

Stopover ecology is another important aspect of migration, shifting the timeframe over which survival is prioritised. For many reasons, stopover habitat selection and

ecology may be hugely influential on migrant populations. As significantly more energy is consumed during flight than can be acquired during stopovers of the same duration (Erni et al., 2002a; Lindström, 1995; Strandberg and Alerstam, 2007), birds adopting an intermittent migratory strategy spend more time at stopovers than actively migrating (Erni et al., 2002a; Hedenström and Alerstam, 1997). Because migration speed is a combination of both stopover and flight time, refuelling efficiency at stopovers greatly influences total migration time (Erni et al., 2002a; Hedenström, 1993). Because fuel deposition rate is a critical factor determining the success of migration (Schaub and Jenni, 2001), the duration and frequency of any stopovers is likely to have onward consequences for survival and also possibly future breeding. Theoretically, birds should only interrupt migration when doing so will positively impact subsequent survival or breeding success (Newton, 2010b).

Birds face many trade-offs at stopover sites. Stopovers must be short enough and few enough to ensure that total migration time is not prohibitively increased, but long enough to allow sufficient reserves to be gained for reaching the next refuelling point. Birds can travel for longer during in a single flight and can reduce stopover frequency if they spend more time acquiring larger fat reserves (Alerstam and Lindström, 1990), but this delays departure and increases total migration time. Mass-dependent predation costs during acquisition increase with stopover duration, and increasing mass too much has implications for predation risk (Dierschke, 2003a; Kullberg et al., 1996; Lind et al., 1999). Eurasian blackcaps *Sylvia atricapilla* have been shown to increase fuel deposition rate and food intake under a higher perceived risk of predation at stopovers (Fransson and Weber, 1997). Shorter stopovers reduce total migration time and may grant the advantage of arriving at the destination before competitors, but stopping over for too little time carries a risk of not depositing enough fat to reach the next suitable refuelling site when crossing large barriers, and also offers less insurance against unpredictable weather events or navigational errors (Davidson and Evans, 1988; Gudmundsson et al., 1991). At stopovers, competition and energetic demands are likely to be high, habitats unfamiliar and energy reserves depleted upon arrival, and therefore optimum habitat selection is crucial (Chernetsov, 2006; Hutto, 1985; Moore and Yong, 1991).

Migrants must stop in areas where fat can be deposited quickly and must adopt the correct foraging behaviours to promote this, especially considering that resources are often seasonal and transient. Changes in body condition are often a reflection of habitat quality stopover sites (Delingat et al., 2009; Dunn, 2000). Migrants may judge their expected refuelling capacity in relation to their migration speed and the quality of the habitats in which they stop (Delingat and Dierschke, 2000). Northern wheatears have been found to be more transient and less territorial in grassland habitats than in beach habitats during stopovers, for example, emphasising a role of stopover habitat variation (Delingat and Dierschke, 2000). Sedge warblers take advantage of aphid infestations for pre-migratory fattening and modify stopover behaviour with spatial changes in food availability (Bayly, 2007; Bibby et al., 1976). Hence, some individuals will remain at sites for long periods to deposit fuel stores equating to 80 – 120% of their lean body mass; yet when food is limited, up to 85% of birds will deposit only minimal stores and depart after a few days (Bibby et al., 1976). Another study on northern wheatears found that when foraging conditions improved, individuals remained in suitable habitats for longer, were more aggressive, and delayed departure, suggesting that migrants are flexible in several aspects of stopover ecology (Dierschke, 2003b). The predation-starvation risk trade-off becomes key to how migration can be optimised at this point (Dierschke, 2003a), and stopover requirements most likely differ between individuals because their fuel stores upon arrival differ also. Consequently, the cues for when to interrupt migration should differ at the individual level (Chernetsov, 2006).

Other considerations further influence stopover ecology. To complicate stopover decisions, search and settling costs often occur when birds first arrive (Hedenström and Alerstam, 1998). These costs occur if migrants lose mass or experience low or no mass gain upon arrival because of difficulties establishing a territory (Klaassen, 1996; Rappole and Warner, 1976), or due to physiological constraints of recovering from long-distance flights, for example (Biebach, 1998; Delingat et al., 2006). These costs are considered to be highly influential on fat deposition rates (Delingat et al., 2006). Evidence for low settling and search costs in northern wheatears suggests that individuals can begin accumulating reserves shortly after arriving, allowing them to

minimise migration time (Delingat et al., 2006). Organs also may need to recover from a loss of mass from migratory flights (Bauchinger et al., 2005), increasing energetic demands.

Competitive interactions may be important in stopover ecology. Large numbers of individuals gather at sites at the same time, greatly depleting local food supplies and potentially influencing spatial and temporal migratory patterns for some species (Lindström et al., 1990; Newton, 2010b). Reflecting this, willow warblers *Phylloscopus trochilus* are more aggressive at stopover sites than during winter (Salewski et al., 2007). Fuel deposition rates in bluethroats *Luscinia svecica* at a stopover was found to correlate with dominance status, as was explained by size differences between individuals (Lindström et al., 1990). Interspecific competition at stopovers has been found in both Neotropical (Moore and Yong, 1991) and Palearctic migrants (Salewski et al., 2007), suggesting that food supplies are indeed limited, although examples of these data are extremely limited. Competition between the sexes can lead to differences in stopover ecology for some species but not others. A simulated experiment with pied flycatchers *Ficedula hypoleuca* suggested that dominant males prevent females from foraging efficiently during stopovers (Moore et al., 2003), reducing their migration speed (Dierschke et al., 2005). Competition is unlikely to explain differential migration between the sexes for some species, however (Dierschke et al., 2005).

A final potentially important consideration in stopover ecology is the health or condition of individual birds. Parasites and pathogens are encountered from crossing many different habitats, compromising survival, breeding success and migratory performance (Garvin et al., 2006; Newton, 2010b). Yellow-rumped warblers *Setophaga coronate* that migrate later have higher parasite loads, for example, and this effect is more pronounced in younger birds. Second-year birds with more parasites were also found to be in poorer energetic condition (DeGroote and Rodewald, 2010).

Predation during migration

Predation strongly influences migratory behaviour for several species (Cimprich et al., 2005; Fransson and Weber, 1997; Lank et al., 2003). *Caldrid* sandpipers migrate rapidly and moult swiftly on the wintering grounds to reduce exposure and vulnerability to migratory predators (Lank et al., 2003). Completing moult and migrating before the arrival of migrant falcons reduces predation risk because the period of increased foraging (necessary to meet the higher energetic demands of moulting and migrating) is undertaken before predators arrive. Juvenile birds can afford to migrate later as they do not moult flight feathers in their first winter. Alternatively, pacific dunlin *Calidris alpina pacifica* delay migration and moult after predators leave (Lank et al., 2003). The accumulation of avian predators at stopovers can have a large impact on migration (Alerstam and Lindström, 1990; Dierschke et al., 2003). Blue-gray gnatcatchers *Polioptila caerulea* and American redstarts *Setophaga ruticilla* move into denser habitat at stopovers under increased predator presence (Cimprich et al., 2005). Often, these non-lethal effects from predation risk are larger than those from direct depredation (Lank et al., 2003; Ydenberg et al., 2004). A decline in the body mass and number of western sandpipers *Calidris mauri* using a stopover in south-western British Columbia was shown to be a likely casual effect of an increasing population of peregrine falcons *Falco peregrinus* (Ydenberg et al., 2004). Here, the increased predation risk has changed migratory behaviour by reducing the duration of stopovers, rather than the number of individuals using the site (Ydenberg et al., 2004). Predator avoidance is therefore a high priority for some migrants and potentially restricts foraging behaviour during migration (Cimprich et al., 2005), with potential implications for body condition. This consequently carries over to influence departure and arrival times and subsequent reproduction (Newton, 2010b). It has even been suggested that some behavioural changes in response to predation risk are contributing to the decline of several migratory shorebird species in North America (Ydenberg et al., 2004).

Moult and migration

The requirement to moult is fundamental in birds, and can be restricted by constraints related to migration such as resource availability and the timing of departures and arrivals. The demand of migrating should not compete with moult, nor should moult impede migratory performance. Replacing feathers is a necessity because poor feather quality reduces the ability to evade predators and increases the metabolic demands of flight by reducing flight performance (Barta et al., 2008; Swaddle et al., 1996). Moulting is, however, one of the most energetically demanding activities aside from migrating and breeding (Jenni and Winkler, 2004), and can both reduce mass and severely impede flight (Haukioja, 1971; Swaddle and Witter, 1997). Merilä (1997) found that fat reserves in goldcrests *Regulus regulus* were larger in the later stages of moult, suggesting that birds in active moult either use fat reserves more rapidly or are unable to store as much fat as those which had completed moult. This suggests that a trade-off exists when allocating resources between moult and migration (Merilä, 1997).

Migrants have adaptations to reduce the impact of moulting on migration. Modelling has predicted that the feathers which are most important for flight, suffer high abrasion, or require less energy to produce are moulted later, for example (Barta et al., 2008). Ideally, birds should moult at times of low stress, such as when there are sufficient resources, when individuals are in good condition, and when flight will not be affected. Phenotypic mass changes occur not only during migration but also when switching priorities from moult to migration (Bauchinger and Biebach, 2006). Passerines use both environmental cues and physiological mechanisms to commence moulting when conditions are favourable (Flinks et al., 2008), and so migration, breeding and moult frequently do not overlap and the demands of each kept relatively distinct (Flinks et al., 2008; Hahn et al., 1992; Kjellén, 1994). Chiefly, diet and latitude determine the time available for moulting (Waldenstrom and Ottosson, 2002). Most migrants are comparatively restricted in the degree of plasticity regarding when they can moult because of the need to finish moulting and breeding before migrating (Flinks et al., 2008). Individuals that breed later are even

more time-limited. A study on the common whitethroat in Sweden before migration found that individuals beginning moult later were more likely to interrupt moulting before migrating, allowing for swifter departure times (Hall and Fransson, 2001). A second moult is then carried out on the wintering grounds (Waldenstrom and Ottosson, 2002). This study highlights the importance of early autumn migration, which is likely to be critical for crossing the Sahara desert before conditions worsen (Hall and Fransson, 2001).

Migratory distance is the best predictor of moult strategy. Short-distance passerine migrants typically moult before migrating, whereas long-distance migrants moult upon reaching the wintering grounds (Kjellén, 1994). A comparative study of 48 European passerines describes faster moult in lighter and more migratory species (De La Hera et al., 2009). Where migratory distance varies within populations, for example in European stonechats *Saxicola rubicola,* there may be relative flexibility in both moult and breeding, with differences between the sexes, and seasonal behaviour may be modified according to individual condition (Flinks et al., 2008). It is hypothesised that some species, the pied flycatcher for example, can change the timing and rate of moult in response to differing environmental conditions between seasons in order to combine breeding and moulting without the need to increase energy expenditure (Artem'ev, 2004). Moult strategies therefore vary widely amongst species in relation to their migratory behaviours (Barta et al., 2008; Svensson and Hedenström, 1999). Chiffchaffs *Phylloscopus colibitus* and willow warblers share very similar biology but differ significantly in moult and migratory strategy. Chiffchaffs are short-distance migrants with one moult each year, whereas willow warblers are long-distance sub-Saharan migrants with two annual moults (Underhill et al., 1992; Weber et al., 2005; Weber et al., 2010). Great reed warblers *Acrocephalus arundinacus* moult rapidly during migratory stopovers, whereas several *Locustella* warbler species have more complex moult strategies and moult after leaving their breeding grounds (Barta et al., 2008; Hedenström et al., 1993).

1.3.2 Winter habitat

Winter habitat is a key determinant of migrant population dynamics. Upon reaching the wintering grounds, the constraints associated with the migratory journey are replaced with new demands such as recovering from long-distance flights, acquiring and defending a territory, choosing when to moult, which habitats to occupy, and how to survive with a different suite of potential competitors and predators. Foraging ecology and habitat selection are important determinants of body condition and thus survival during winter, where optimising short-term self-maintenance becomes priority over rapid energy acquisition, at least until priorities shift towards prioritising energy gain and survival towards the end of winter in preparation for return migration. Body condition upon arrival at the breeding grounds must also be considered. The optimal body condition promoting survival and fitness therefore fluctuates throughout winter – from recovery on arrival, to survival over the winter, and finally during preparation for the return journey to the breeding grounds.

Winter habitat preferences

Habitat preferences on the wintering grounds are generally species-specific (e.g. Jones et al., 1996b; Wilson and Cresswell, 2006), and differ between the Palearctic and Neotropics (Böhning-Gaese and Oberrath, 2003). In the Palearctic, habitat preferences are often reflected in aspects such as vegetation structure (Pearson and Lack, 1992; Spina et al., 2006). Migrants are typically associated with open woodlands and seasonal savannahs, and within them use resources that are typically abundant and not used by specialist resident species (Leisler, 1992). In the Neotropics, many migrants are associated with forest habitats (Böhning-Gaese and Oberrath, 2003). In both regions, the density of several migrant species has been found to differ with habitat type, and this can differ between age and sex classes (Jones et al., 1996b; Newton, 2010a; Sherry and Holmes, 1996; Wunderle Jr, 1995). Tree density is an important indicator of habitat suitability for a range of species, especially in the Palearctic (Cresswell et al., 2007; Jones et al., 1996b; Stevens et al.,

2010; Wilson and Cresswell, 2006), along with other characteristics such as fruiting shrubs (Wilson and Cresswell, 2006).

The majority of Palearctic migrants – over 70% of individuals and almost half of the total migrant species – winter in the northern tropics (Brown et al., 1982; Curry-Lindahl, 1981; Elgood et al., 1966; Lack, 1990). The number of individuals and species becomes less further south (Jones et al., 1996a). Most migrants arrive during the dry season (Jones, 1995; Sinclair, 1978). In East Africa, most associate with dry bush and woodland below 2000 metres, although exceptions exist (Pearson and Lack, 1992). Tree pipits *Anthus trivialis*, Eurasian blackcaps, chiffchaffs, and grey wagtails *Motacilla cinerea* are often found in higher montane forests, whereas wood warblers *Phylloscopus sibilatrix* and golden orioles *Oriolus oriolus* prefer low attitude rainforest canopies (Pearson and Lack, 1992). Many species wintering in the Serengeti are associated with areas where it has recently rained (Sinclair, 1978), and throughout the wintering quarters several migrant species associate with farmland and other human-modified or degraded habitats, both in Africa (Barshep et al., 2012; Hulme and Cresswell, 2012; Jones et al., 1996b; Stevens et al., 2010), and in the Neotropics (Wunderle Jr and Latta, 2000). In Africa, the tendency of species to be only loosely associated with specific habitat features and types suggests that migrants are able to utilise a wide-range of habitats (Stevens et al., 2010; Wilson and Cresswell, 2006).

Winter habitat, predation and body condition

Winter habitat selection upon arrival and throughout winter is key for both overwinter survival and the success of subsequent migration (Gunnarsson et al., 2005). High metabolic rates and small body size mean that, for many migrants, fat stores are essential for short-term survival (Chaplin, 1974), and birds typically operate on a diurnal cycle of early and late foraging to recover from and prepare for overnight starvation (Hurly, 1992). Higher reserves generally reflect better body condition and survival probability in an unpredictable environment, although paradoxically, all things being equal, an individual that can survive while maintaining

lower reserves is likely to be the better competitor, because maintaining energy reserves is costly (Cresswell, 2009; Houston et al., 1997; Lima, 1986; Witter and Cuthill, 1993). Birds optimise body condition to maximise survival and future fitness by correctly balancing the trade-off between starvation and predation risk with respect to foraging conditions, resource availability, variation in predation risk, and each life history stage (Lima, 1986). Consequently, migratory birds demonstrate great variation in mass depending on whether they are fuelling for migration or resident on either their wintering or breeding grounds (Bauchinger et al., 2005; Houston and McNamara, 1993; Houston et al., 1997; Piersma et al., 1995; Scott et al., 1994; Yohannes et al., 2008). Mass varies along migratory routes, specific to seasonal demands (Yohannes et al., 2008), and migrants typically depart from sites along the migratory path with a higher mass than on arrival (Dunn, 2002; Hedenström and Alerstam, 1997; Karason and Pinshow, 1998).

Habitat quality influences body condition, and therefore survival, through resource availability and accessibility (Cresswell, 2009), which are also determined to some extent by predation risk (Lima, 1986). Consequently, body condition is often a reflection of habitat quality. To maximise survival and maintain adequate body condition, migrants must therefore consider in which habitat or region to reside during the non-breeding season, and whether to remain in one area or move to others (Pearson and Lack, 1992). Migration is an excellent example of how environmental variation leads to changes in the relationship between body condition and fitness. Higher quality environments may allow individuals to be more flexible when they forage and may allow them to feed at times and in areas where predation risk is lower, whereas poorer habitats force individuals to forage even when predation risk is high in order to gain sufficient reserves (Cresswell, 2009). Generally, poorer environments increase the optimal reserve levels required to survive from one period to the next (McNamara and Houston, 1990). Individuals in very poor habitats often exhibit a mass-dependent response, in which they reduce fat reserves and thus predation risk by reducing foraging time (and so time exposed to predators) and increasing flight and escape performance (due to increased acceleration associated with lower mass) (Cresswell, 2009; Kullberg et al., 1996; Witter and

Cuthill, 1993). Habitats with higher food abundance but higher predator densities may result in similar responses with respect to body condition as those habitats with low resources and fewer predators. This is because foraging is compromised and therefore foraging gain reduced, despite high resource availability, and so birds in seemingly good habitats may be in a similar condition to those in poorer habitats. A mass-dependent response is only favoured over a interrupted foraging response if poor habitat quality prevents individuals from gaining the sufficient energy reserves that an interrupted foraging response demands (Brodin, 2007; Cresswell, 2009). It is therefore expected that in areas where predation risk is known or constant, mass can be used as an indicator or reflection of habitat quality (Benson and Bednarz, 2010; Cresswell, 2009; MacLeod et al., 2008). However, the relationship between mass, fitness and the environment is context-dependent and may be more complex (Cresswell, 2009). Several Palearctic species also undergo rapid moult on the wintering grounds in response to the limited period of food availability before the oncoming dry season (Bensch et al., 1991; Hedenström et al., 1993), with further implications for body condition and consequently habitat choice. A study on garden warblers on their wintering grounds found that birds that had completed moulting and were ready to depart for spring migration had larger flight muscles than those still undergoing body moult (Bauchinger and Biebach, 2006). Studies in the Neotropics highlight the importance of body condition over winter (e.g. Marra and Holmes, 2001; Reudink et al., 2009); however the lack of data in this area, along with very limited data on Palearctic migrants (particularly their level of predation risk on the wintering grounds), emphasises the need for more research.

Seasonal changes

Because of the seasonal climate of the tropics, non-breeding habitats can alter significantly during the time that migrants are present. Such temporal changes in food availability further influence body condition and survival. A substantial decline in mass relating to the dry season has been observed in American redstarts, with greater reductions observed in poorer habitats (as determined by having lower populations) (Sherry and Holmes, 1996). To avoid the costs of moving (see below),

migrants must be flexible and adaptable to changing conditions. In the Sahel, some migrants may favour tree species that maintain constant invertebrate densities throughout the winter, such as evergreen tree species, rather than deciduous trees in which invertebrate densities decline as the dry season progresses (Wilson and Cresswell, 2006). Nevertheless, some species show movement throughout the winter, most likely in response to changing conditions (Jones, 1995). Many migrants follow the intertropical rain belt during the winter to benefit from humid conditions (Åkesson et al., 2012; Delmore et al., 2012; McKinnon et al., 2013a; Pearson, 1990).

Competition

Competition between and within species is another factor that may also influence population dynamics during the non-breeding season (reviewed by Greenberg, 1986). Migrants typically use a wider suite of resources and reside in more open habitats compared to similar resident species, (Leisler, 1992). Interspecific competition for resources is thought to be less influential on the wintering grounds than at stopovers, with little evidence of interspecific competition during winter; however few studies have investigated competition on the wintering grounds in detail (Leisler, 1992; Salewski et al., 2007; Salewski et al., 2002a, 2003; Salewski et al., 2002b; Wilson and Cresswell, 2010b). Wilson and Cresswell (2010) in fact found a positive correlation between occurrence of Palearctic and Afrotropical species. A study comparing pied flycatchers and willow warblers with wintering residents in Africa suggests that Palearctic and resident species coexist because migrants are more flexible in their foraging behaviours, habitat choice, and consequential resource partitioning (Salewski, 2000; Salewski et al., 2003). The preference migrants have for open seasonal habitats further reduces interspecific competition (Herremans, 1997; Leisler, 1992; Salewski et al., 2002a). Intraspecific competition between conspecifics may, however, be more prevalent. Many migrants wintering in Africa and in the Mediterranean are territorial (Barshep et al., 2012; Cuadrado, 1997, 1995; Dejaifve, 1994; Kelsey, 1989; Pearson and Lack, 1992; Salewski et al., 2007; Salewski et al., 2002a). For example, marsh warblers *Acrocephalus palustris* are territorial for longer periods in Africa than during summer, most likely because

territoriality acts to defend long-term resources (reliable food resources) rather than short-term resources (breeding females) (Kelsey, 1989). Territoriality during the non-breeding season also frequently occurs in the Neotropics (Rappole, 1995).

Finding suitable habitat: the implications of being a migrant

Migrants face the unique challenge of finding, sampling, and overwintering and migrating in habitats and during conditions that cannot be predicted from the breeding grounds. Often, numerous habitat types are used throughout the annual cycle (Chernetsov, 2006). For the majority of small passerine migrants, migration and site selection in the first winter is likely to be relatively stochastic at a large scale within the wintering range because individuals have no prior knowledge of wintering conditions (Cresswell, 2014), or of stopover habitats (Chernetsov, 2012a; Hutto, 1985). As already established, both stopover and winter habitat selection and use are fundamental to the success of migration, survival and future reproduction, and habitat selection must be efficient and rapid if individuals are to maximise their survival (Chernetsov, 2006). In response to unpredictable conditions, migrants often sample habitats at stopovers, hold territories, or roam across larger areas, and may search and settle in different areas before using a specific habitat (Chernetsov, 2006). Which habitat is chosen is likely to depend upon body condition (Chernetsov, 2006). Migrants often land at the end of the night when visual habitat selection is easier (Bolshakov and Rezvyi, 1998), and select stopover locations during daylight (Moore and Aborn, 2000; Moore et al., 1995). Using conspecifics as cues for suitable habitat further increases efficiency over direct habitat sampling (Mönkkönen et al., 1999). High site fidelity is one strategy to lessen the costs of unpredictable conditions (Cresswell, 2014), as will be discussed; yet this strategy does not necessarily safeguard against habitat change between years.

Non-breeding habitat and migrant declines

Long-distance migrants have been found to be especially vulnerable to changes in winter habitat conditions (Ockendon et al., 2012; Ockendon et al., 2014; Sanderson

et al., 2006; Zduniak et al., 2009). Rainfall on the wintering grounds is particularly influential because of its role in creating the non-arid habitats on which many migrants rely (Szep, 1995a, b). Severe droughts in the Sahel from 1965 to 1970 have been linked to the 80% population decline in the British population of common whitethroats at the end of the 1960s (Baillie and Peach, 1992; Winstanley et al., 1974). Annual survival rates of many Palearctic migrants have been found to positively correlate with annual rainfall in the Sahel (Cowley and Siriwardena, 2005; Ockendon et al., 2012; Ockendon et al., 2014), and droughts in Sahelian areas have had a large detrimental effect on both Hungarian (Szep, 1995b) and Central European populations of sand martins (Szep, 1995a). Sedge warblers have also shown dramatic declines that can be attributed to yearly rainfall in the western Sahel-Sudan zone (Foppen et al., 1999).

Consequently, habitat degradation and loss outside of the breeding season is a principle driver of declines for some migrants (Berthold, 2001; Böhning-Gaese, 1992; Newton, 2004; Sanderson et al., 2006; Vickery et al., 2014). Many declining species winter in the arid zone of the African Sahel, suggesting that recent habitat loss and degradation in this region – caused by reduced rainfall and increased agricultural intensification (e.g. see Cresswell et al., 2007; Wilson and Cresswell, 2006) – may be a significant driver of their declines (Berthold, 2001; Nicholson et al., 2000; Sanderson et al., 2006). A reduction in the density of *Salvadora* fruits, for example, which are an important resource for pre-migratory fattening for several migrants, is likely during droughts and under increased grazing pressure (Wilson and Cresswell, 2006), and could have a large impact on some migrant populations (Stoate and Moreby, 1995). In the Neotropics, migrant declines have been linked to the loss of tropical forests. Habitat degradation leads to reduced food availability and reduced habitat quality, both of which have been shown to limit migrant populations in the Neotropics (Norris et al., 2004; Sherry et al., 2005). Likewise, in the Palearctic system, a likely indicator of food availability is a change in the pattern of rainfall and primary production in the Sahel, both of which have been linked to declining migrant populations (Baillie and Peach, 1992; Kanyamibwa et al., 1990; Peach et al., 1995; Sanderson et al., 2006; Szep, 1995a, b). The influence of African rainfall on migrant

populations implies that seasonal food resources on the wintering grounds have a key impact on the population dynamics of migrants (Ockendon et al., 2014).

Studies that have shown that several migrant species complete for winter habitat of varying quality or show dominance-based habitat segregation, and that winter habitat can influence future breeding success, further suggest that winter habitat can limit migrant populations (Catry et al., 2004a; Herremans, 1997; Marra et al., 1998; Nisbet and Medway, 1972; Sherry and Holmes, 1993; Sherry and Holmes, 1995; Studds and Marra, 2007). Yet despite these links, recent studies in Africa suggest that for some species winter habitat may not be as limiting as first thought (Hulme and Cresswell, 2012; Jones et al., 1996b), and in fact the wintering period is relatively stress-free compared to breeding and migrating (Kok et al., 1991). Furthermore, considering that species that do not pass through the Sahel region are also declining, the degradation of the Sahel cannot be the sole driver of declines (Sanderson et al., 2006). A recent study on 46 years of data revealed that breeding conditions influenced reproductive traits more so than wintering conditions for many migrants (Ockendon et al., 2013). Although the negative influence of habitat loss and degradation on migrant populations is clear, the relationship between wintering conditions and migrant declines is likely to be complex. Most likely, the extent at which migrant populations are affected differs between the Neotropic and Palearctic systems (e.g. Jones and Cresswell, 2010) and is species and population-specific. What is clear is that data are lacking, especially for the Palearctic system and at the population and species-level.

1.4 Site fidelity

The degree to which a migrant is site faithful – where individuals reside in or return to the same area used in a previous migration – is fundamental to migrant population dynamics. Important factors affecting winter survival are the ability to find and defend food resources and previous experience of the wintering site (Belda et al., 2007; Cuadrado et al., 1995), both of which increase with the scale of site fidelity. The benefits of site fidelity also increase if resources are more predictable.

Fundamentally, there are risks to both moving during the winter and remaining in the same area. Moving can reduce survival because individuals often risk higher predation in unfamiliar surroundings and the ability to find food is compromised (Cresswell, 2014; Cuadrado, 1997; Hedenström, 2008; Lind and Cresswell, 2006; Piper, 2011; Yoder et al., 2004), and returning to the same site between winters ensures prior knowledge of foraging habitats, competitors and predators (Catry et al., 2004b; Nisbet and Medway, 1972). Yet remaining in the same area demands that individuals are flexible should conditions change, and they cannot benefit from tracking the best or most accessible resources, the distribution and location of which often changes throughout the winter. Consequently, site fidelity has been shown to occur on a range of scales in both the Palearctic and Neotropics (Terrill, 1990), from species remaining in the same territory throughout the winter to being itinerant and moving to follow food resources (Belda et al., 2007; Cresswell et al., 2009; Newton, 2010b; Pearson and Lack, 1992; Pérez-Tris and Tellería, 2002).

Many migrants have been shown to use the same wintering sites year on year (e.g. Catry et al., 2004b; Cresswell, 2014; Cuadrado et al., 1995; Holmes and Sherry, 1992; Nisbet and Medway, 1972). Many show high site fidelity during the winter by holding discrete territories during some or all of the wintering season (Barshep et al., 2012; Belda et al., 2007; Cuadrado, 1997, 1995; Dejaifve, 1994; Kelsey, 1989; Pearson and Lack, 1992; Salewski et al., 2007; Salewski et al., 2002a). Several studies have found that blackcaps return to the same wintering sites in Spain (Cuadrado, 1992; Cuadrado et al., 1995), as do European robins (Cuadrado, 1992). Subalpine warblers *Sylvia cantillans* and common whitethroats return to the same wintering sites in the Gambia (King and Hutchinson, 2001), Eastern great reed warblers *Acrocephalus orientalis* return to exactly the same home ranges on their wintering grounds in Malaysia (Nisbet and Medway, 1972). Common whitethroats and marsh warblers return to the same stopover sites in East Africa (Yohannes et al., 2007). Whinchats *Saxicola rubetra* hold discrete territories throughout the winter (Barshep et al., 2012). Black-tailed godwits select wintering habitats independent of adults and return to the same wintering site each season (Gunnarsson et al., 2005). In the Neotropics, black-throated blue warblers *Setophaga caerulescens* and American

redstarts have been found to show similar site fidelity on the wintering grounds, and show a higher degree of site fidelity on the wintering than breeding grounds (Holmes and Sherry, 1992). Many geese, swans and sea ducks also return to the same wintering areas (Robertson and Cooke, 1999), and there are many more examples (see Cresswell, 2014). Fundamentally, the implications of selecting high quality wintering sites likely increases with the degree of site fidelity.

A significant number of migrants also show seasonal movements throughout the winter. Pearson (1990) documents movements of 21 species of Palearctic migrants, some of which migrate an additional 6,000 – 10,000 km south during the winter. Other migrants have also been shown to move southward during the non-breeding season (Cresswell et al., 2009). Many migrants wintering in East Africa have been found to move south to exploit resources as the wintering season progresses, such as the non-*Sylvia* warblers, flycatchers, swallows and non-passerines (Pearson and Lack, 1992). Note that these movements may be between distinct sites that are revisited each year in succession (see below). Most likely, these movements are in response to changing resource availability and the different conditions found in different areas at different times of the year (Pearson, 1990; Pearson and Lack, 1992). Wintering in sub-optimal habitats has been shown to lower reproductive success for some migrants (Norris et al., 2004; Reudink et al., 2009), implying that species can benefit from relocating. Several migrants move in direct response to climatic conditions (Cresswell et al., 2009; Hedenström et al., 1993; Moreau, 1972; Pearson and Lack, 1992; Sinclair, 1978), such as different spatial and temporal patterns of rainfall (e.g. Cheke et al., 2007; Cresswell et al., 2009; Saino et al., 2007; Wisz et al., 2007). Harsh conditions may be avoided by moving south into wetter and more productive habitats (Cresswell et al., 2009; Moreau, 1972; Sinclair, 1978), especially as insect abundance in Africa is often strongly linked with rainfall (Denlinger, 1980). In the Serengeti, many species that arrive in areas where there has been recent rainfall will move to wetter areas if conditions dry out (Sinclair, 1978). Typically, the species likely to move south are those that prefer wetter habitats, and they are likely to be restricted to small areas as a result, such as river warblers *Locustella fluviatilis* and marsh warblers wintering in Kenya, for example

(Pearson and Lack, 1992). Some species may be more itinerant during the winter, such as willow warblers, tree pipits and garden warblers (Newton, 2010b; Salewski and Jones, 2006). Although moving allows migrants to track resources as a result of temporal changes in resource availability, moving can also increase the distance needed to travel back to the breeding grounds. As a result, and most likely because of adaptations to harsher conditions, many migratory species remain north, such as the *Sylvia* warblers, chats, larks, buntings and wheatears (Pearson and Lack, 1992).

To compensate for seasonality but to benefit from site fidelity, some migrants may have multiple wintering sites, and so the number of wintering sites can vary between individuals of the same species and also between migratory stages. Migrant blackcaps have been shown to be both resident and transient during winter (Belda et al., 2007). Mixed wintering strategies have been found in chiffchaffs (Catry et al., 2003) and siskin *Spinus spinus* (Senar and Metcalfe, 1988). Belda et al (2007) estimated that only 28% of blackcaps showed winter site fidelity at a site in Valencia. Catry et al. (2004) argue that fidelity to stopover sites is less important if sites are far from winter or summer grounds. Species can vary in the degree of within-winter site fidelity and use multiple wintering sites, remaining territorial at each and then relocating (Åkesson et al., 2012; Delmore et al., 2012; Eraud et al., 2013; Heckscher et al., 2011; McKinnon et al., 2013a; Stach et al., 2012; Tøttrup et al., 2012). By using multiple wintering sites, individuals likely benefit from both territoriality during the winter and the ability to track resources. This strategy does not, however, avoid the costs of relocating.

1.5 Individual variation

Regardless of the constraints of migration, individual variation in quality, condition, competitive ability, resilience to pathogens and experience will result in different optimal strategies between individuals of the same species. Particularly, the age and sex of an individual can influence morphology and body condition, and constraints and priorities often differ with age and sex, especially during breeding.

The influence of age

Age influences the strength of many of the constraints acting on migrants. Variation in the timing of migration between different age and sex classes has been reviewed by Gauthreaux (1982) . Birds of different age classes migrate at different speeds, both waders (Remisiewicz and Wennerberg, 2006; Saurola, 1980) and small passerines such as willow warblers (Hedenström and Petterson, 1987) and bluethroats (Ellegren, 1990, 1991). Younger wood sandpipers *Tringa glareola* migrate later than older birds (Remisiewicz and Wennerberg, 2006). It is well documented that the problems and pressures encountered during migration are greater for yearling birds (DeSante, 1983; Lindström and Alerstam, 1986; Ralph, 1978; Woodrey and Moore, 1997). Individuals undertaking their first migration are likely to be less proficient at meeting energetic demands, resulting in less efficient fattening in preparation for flight and at stopovers, or higher fat reserves as insurance against starvation risk (Woodrey and Moore, 1997). For example, adult bluethroats have a more concentrated migration period than juveniles, even though both age classes commence migration at the same time (Ellegren, 1991). At stopovers, several studies have found that adults carry more fat, stopover for less time, maintain better body condition and begin depositing fat earlier than younger birds (Ekholm, 1982, 1988; Ellegren, 1991; Lindström and Hasselquist, 1989). Adult pied flycatchers have been found to carry larger fat reserves than juveniles (Veiga, 1986). Neotropical migrants also show age-related differences in fat load (Woodrey and Moore, 1997). Adults of several Nearctic warblers carry more fat than youngsters (Murray, 1979). Older Swainson's thrushes *Catharus ustulatus*, white-eyed vireos *Vireo griseus* and American redstarts carry more reserves than young birds, so much so that only older birds carry the sufficient reserves to make non-stop flights over large barriers such as the Gulf of Mexico (Woodrey and Moore, 1997). By having lower reserves, younger birds have time and energy to invest during migration and suffer reduced migratory performance as a result (Curio, 1983; Woodrey and Moore, 1997).

Adults also often arrive earlier on the breeding grounds than sub-adults (e.g. Francis and Cooke, 1986; Hill, 1988; Lozano et al., 1996; Spina et al., 1994) and breed more successfully as a result (Lozano et al., 1996). Adult male American redstarts, for example, are more likely than sub-adults to mate and have nests within their territories because of their earlier arrival (Lozano et al., 1996). An investigation of Palearctic migrants in Italy found that adult birds arrive before yearlings for 18 of 26 species (Spina et al., 1994). Older male northern wheatears arrive earlier on breeding grounds in Stockholm and occupy territories most suited to their forging strategy (Brooke, 1979). Older barn swallows have been found to remain on their wintering grounds for longer if ecological conditions improve, suggesting that individuals of different ages respond differently to conditions on the wintering grounds but not en route (Balbontin et al., 2009). For many reasons, including greater experience, older birds are often considered to be more efficient at migrating than juveniles (Ellegren, 1991; Lozano et al., 1996).

Differences between the sexes

Differences in migratory strategy occur between the sexes of many species, for many reasons, such as differing requirements on the wintering grounds (Ketterson and Nolan Jr, 1983), differences in migration speed and physiology (Chandler and Mulvihill, 1990; Swanson et al., 1999), higher fat deposition rates for males (Dierschke et al., 2005), differences in the timing of departure to the breeding grounds (Dierschke et al., 2005; Moore et al., 2003; Wood, 1992), and size differences between males and females (Francis and Cooke, 1986). The considerations and constraints that influence birds on the breeding grounds also vary considerably between the sexes, and this carries over to influence ecology year-round. Observations such as these have led to the generalisation that males operate on a time-minimisation strategy to optimise migration, more so than females (Dierschke et al., 2005). Male northern wheatears migrating to Greenland or Iceland show a positive correlation between deposition rates and fat load on departure, whereas females continue migration irrespective of fat stores, suggesting that males alone are time minimisers (Dierschke et al., 2005). Catry and Bearhop (2007) found

that the majority of chiffchaffs at a wintering site in Portugal were female, whereas the sex ratio of transient birds was equal. Furthermore, females maintained body condition for longer, had higher muscle mass and commenced moulting sooner, suggesting that males either arrive in poorer quality or have inferior competitive ability over females (Catry et al., 2007). Some species such as European robins show strong differential migration according to sex, with males and females migrating to different areas (Catry et al., 2004a). The effect of Sahelian rainfall on annual survival rates of sand martins has been found to be greater for females than males (Szep, 1995b), suggesting that the effect of conditions during winter are different for males and females.

A significant difference is that males often arrive at breeding and wintering grounds before females (Potti, 1998; Remisiewicz and Wennerberg, 2006; Spina et al., 1994). Differential timing in arrival dates between the sexes is believed to be because the benefits of arriving early are greater for males (Chandler and Mulvihill, 1990; Dierschke et al., 2005; Francis and Cooke, 1986; Myers, 1981; Spina et al., 1994). Earlier arrival allows males to take advantage of resources and suitable conditions as soon as they are available, whereas females time their arrival dates with the start of nesting (Chandler and Mulvihill, 1990; Francis and Cooke, 1986; Myers, 1981). A large study in Italy found that males arrive significantly earlier than females for 13 of 16 Palearctic migrant species (Spina et al., 1994). Failure to secure a high-quality breeding territory reduces survival probability and influences several aspects of breeding success because the chances of acquiring a mate or successfully raising a clutch to fledging are reduced due to poor food availability (Lack and Gillmor, 1966). Modelling has suggested that female American redstarts in lower quality territories will produce at least two fewer young and fledge offspring up to one month later, for example (Norris et al., 2004).

These patterns are not the same for all migrants, however. Female curlew sandpipers *Calidris ferruginea* depart their breeding rounds 21-35 days later than males and stay at stop-over sites for less time, resulting in faster migration speed than males (Figuerola and Bertolero, 1998). Females typically increase reproductive

success from earlier arrival on the breeding grounds through earlier egg-laying dates (Hasselquist, 1998; Smith and Moore, 2005). Female northern wheatears have been found to time the start of breeding with the timing of their arrival in Sweden (Brooke, 1979), indicating the advantage of early arrival. Different migratory strategies between sexes has been found in many non-passerine species such as semipalmated sandpipers (Lyons and Haig, 1995) and western sandpipers (Warnock and Bishop, 1998). Female pectoral sandpipers *Calidris melanotos* deposit more fat during migration than males, which is likely to improve breeding performance later in the season (Farmer and Wiens, 1999). Increased fat reserves during migration may buffer against the costs of incubation (MacLean, 1969) or allow females to produce larger eggs and therefore larger nestlings (Farmer and Wiens, 1999).

1.6 Migratory connectivity and carry-over effects throughout the annual cycle

The different stages of breeding, migrating, and wintering are far from distinct (Webster et al., 2002). The degree of migratory connectivity – the geographical links between breeding and wintering areas (Webster et al., 2002) – can have significant implications for the ecology, conservation and population dynamics of migrants, and the different stages of the annual cycle can influence future survival and reproduction success through seasonal interactions and carry-over effects.

Migratory connectivity

The degree of migratory connectivity varies significantly between migratory species and likely between the Palearctic and Neotropics. Migratory connectivity is strong (i.e. occurs on a small scale) if individuals from and one breeding population share similarities in their migratory behaviour and the location of their wintering quarters (i.e. at a scale less than 1000 km). This is likely to occur if individuals are affected by similar environmental conditions during migration, or if social learning is present, as is the case for some larger non-passerine species (Cresswell, 2014). Strong connectivity can mean that whole populations can be affected by events occurring in any one location used during the annual cycle. Low migratory connectivity (i.e.

connectivity on a large scale or no connectivity), in which individuals from the same breeding or wintering population do not spend the migratory cycle in the same or similar geographical locations, means that the impact of events at one location (or on a relatively small scale such as <1000km) will not affect the entire population. If individuals that breed in one location also winter together, conservation efforts may be made more effective by focussing on a small number of critical breeding or wintering locations (Webster et al., 2005). Migratory connectivity also has implications for how individuals and populations adapt to changes occurring at non-breeding locations by determining the degree of gene flow between populations wintering in the same location. The degree of migratory connectivity therefore has implications for understanding the ecology and evolution of migrants, population genetics and gene-flow, the degree to which migrants are locally adapted to their wintering locations, the degree to which different selective pressures influence migrants at the population or species-level, determining and understanding the rate of any fluctuation in wintering ranges, and for focussing conservation efforts (Webster et al., 2005). The strength of migratory connectivity has been linked to the extent of population declines in cerulean warblers *Setophaga cerulea*, for example (Jones et al., 2008). We would expect the relatively stochastic nature of site selection within the wintering range in the first winter for small passerine migrants and differences in the timing of migration between adults and juveniles to result in relatively low migratory connectivity in the Palearctic system (as hypothesised by Cresswell, 2014).

Our understanding of the degree of migratory connectivity has been greatly improved by recent studies using geolocators to track migrants throughout the annual cycle (see examples within McKinnon et al., 2013a). Generally, the degree of migratory connectivity is lower in the Palearctic than Nearctic, most likely because the total land area within the Neotropics available for wintering is lower, thus forcing individuals into smaller limited areas (Cresswell, 2014). Eurasian hoopoes *Upupa epops* have low migratory connectivity, with individuals from the same breeding population varying widely in their migratory behaviour and the location of their wintering areas (Bächler et al., 2010). Common redstarts *Phoenicurus*

phoenicurus (Kristensen et al., 2013), purple martins *Progne subis* (Fraser et al., 2012) and great reed warblers (Lemke et al., 2013) have all been shown to have low migratory connectivity (but see Cresswell, 2014 for more examples). In contrast, Swainson's thrushes have been shown to have relatively high migratory connectivity (Delmore et al., 2012), as have Wilson's warblers *Wilsonia pusilla* (Clegg et al., 2003), gray catbirds *Dumetella carolinensis* (Ryder et al., 2011), American redstarts (Norris et al., 2006), Bicknell's thrushes *Catharus bicknelli* (Hobson et al., 2004) and yellow warblers *Setophaga petechia* (Boulet et al., 2006).

Carry-over effects

For many migrants, ecology, behaviour and condition during one stage of the annual cycle influence survival in the next and carry over to influence future reproductive success. Primarily, this is because the constraints placed on migrants during winter and the migratory journey influence body condition (Bearhop et al., 2004; Marra et al., 1998; Webster et al., 2002). Because of the relationship between better body condition and higher breeding success (see references within Chastel et al., 1995), body condition upon arrival on the breeding grounds and throughout winter can be central to annual reproductive success, especially for long-distance migrants and for single brooded species with typically small clutches (e.g. Bearhop et al., 2004; Marra et al., 1998; Norris et al., 2004). Conditions during migration itself such as wind speed can also carry-over to influence several aspects of breeding ecology and future reproduction (Drake et al., 2014), most likely by reducing the reserves needed to complete migration, or by determining reserves that remain after migration that can then be used for breeding. Fundamentally, energy reserves upon arrival allow more resources to be allocated to reproduction (Bearhop et al., 2004; Smith and Moore, 2003). Females in better condition are more capable of producing, incubating and raising a clutch (Aldrich and Raveling, 1983; Wiggins et al., 1994a), whereas males in better condition are likely to be at a competitive advantage, especially for species which are territorial.

Conditions during winter and spring migration also affect breeding success by influencing spring arrival dates (Bearhop et al., 2004; Delingat et al., 2006; Marra et al., 1998; Møller, 1994; Norris et al., 2004; Webster et al., 2002). Birds migrating with more reserves may migrate more rapidly by reducing the time required to replenish reserves at stopovers, and so may reach the breeding grounds first. Arrival time at the breeding grounds is linked with many aspects of migration and is a key determinant of breeding success (e.g. Brooke, 1979; Delingat et al., 2006; Gordo, 2007). Migrants typically have a limited period to breed (Both et al., 2006b; Ramenofsky and Wingfield, 2006), placing selective pressure on both optimal arrival and the timing of reproduction (e.g.Bauchinger et al., 2009; Lozano et al., 1996; Møller, 1994; Newton, 2007; Smith and Moore, 2005). Arrival dates must allow time to establish a territory, track favourable conditions and resources, and commence early breeding to maximise the number of young fledged (Lozano et al., 1996). For males, earlier arrival can give a competitive advantage when establishing the best territory and increase the likelihood of securing a mate or fledging young (Lozano et al., 1996). Arrival dates are also often strongly linked with peak food availability, the significance of which is highlighted by recent studies on the impact of climate change on migrant bird populations (e.g. Both et al., 2005; Both et al., 2006a; Both and Marvelde, 2007; Both et al., 2010; Jones and Cresswell, 2010). Conditions on the wintering grounds may also determine when migrants are able to depart. Northern wheatears breeding in Stockholm begin laying three weeks after arrival (Brooke, 1979), and so their breeding success may be linked the ability to depart early from the wintering grounds. Weather conditions on both the wintering and breeding grounds have been found to influence male arrival dates (Møller, 1994; Norris et al., 2004). Generally, males of higher phenotypic quality often arrive earlier than poorer quality males (Forstmeier, 2002; Marra et al., 1998; Møller, 2001; Møller, 1994). After breeding, body condition upon arrival the wintering grounds must also be considered, because arriving in poor condition on the wintering grounds may increase predation or starvation risk or cause failure to compete for a high-quality wintering territory.

There is, however, a trade-off associated with arrival times. Costs occur from arriving too early, such as increased mortality due to poor weather conditions for males (MacLean, 1969; Møller, 1994) and those associated with breeding too early for females (Visser et al., 1998). For example, sub-Arctic and Arctic breeding shorebirds arriving too early will encounter frozen foraging habitats, resulting in a loss of body condition which is detrimental to onward migration and reproduction, and an increased risk of mortality (Green et al., 1977; MacLean, 1969). The costs of early arrival are often greater for birds in poorer condition (Kokko, 1999; Møller, 1994).

Winter habitat quality in particular has been shown to carry over to influence many migrants during the breeding season (e.g. Bearhop et al., 2004; Inger et al., 2008; Marra et al., 1998; Sherry and Holmes, 1993; Webster et al., 2002). Ecological conditions at staging sites have been shown to affect when barn swallows arrive at their African wintering grounds and at stopover sites in North Africa, where more favourable ecological conditions at staging sites result in earlier arrival at stopover sites and delayed arrival at the wintering grounds (Balbontin et al., 2009). Female American redstarts arriving on their breeding grounds with low fat reserves suffer reduced reproductive success (Smith and Moore, 2003). Conditions during winter and during migration influence body condition and arrival date for palm warblers *Setophaga palmarum* and northern waterthrush *Parkesia novaboracensis* (González-Prieto and Hobson, 2013). Earlier arrival allows for the acquisition of a higher quality territory and increased breeding and mating success for barn swallows (Møller, 1994), great reed warblers (Hasselquist, 1998), northern wheatears (Brooke, 1979; Currie et al., 2000), pied flycatchers (Lundberg et al., 1981), willow warblers (Gil and Slater, 2000), dusky warblers *Phylloscopus fuscatus* (Forstmeier, 2002) and American redstarts (Lozano et al., 1996). In a study of arrival dates from 1982 to 2000, Gordo and Sanz (2007) found that ecological conditions such as higher resource availability on the wintering grounds influenced spring arrival dates for white storks *Ciconia ciconia*, common cuckoos *Cuculus canorus* and barn swallows (Gordo and Sanz, 2007). Winter habitat quality carries over to affect breeding success through the number of young fledged for American redstarts (Norris et al., 2004). Temperature on the wintering ground has been found to be particularly

important for later arriving species such as common cuckoo, common swift *Apus apus* and nightingales *Luscinia megarhynchos* (Gordo and Sanz, 2007) because higher habitat productivity over winter likely increases survival rates and allows rapid accumulation of fat deposits and therefore faster migration.

1.7 Additional drivers of decline

Climate change

The effect of climate change, be it natural or anthropogenic, also contributes to migrant declines, with far reaching implications both in terms of habitat suitability, migration, phenological mismatch between the wintering and breeding grounds (Both et al., 2010; Jones and Cresswell, 2010; Saino et al., 2011), and competition with resident species (Ahola et al., 2007). A major consequence is the advance of spring and the delay of autumn (Menzel et al., 2006; Schwartz et al., 2006). If warming or cooling occurs at different rates between wintering and breeding areas, migration may be delayed and the start of the breeding season may be missed (Jones and Cresswell, 2010). Alternatively, migrants may migrate before conditions become suitable, and the consequences can be detrimental (Møller, 1994). Long-distance migrants, especially those wintering in sub-Saharan Africa, are suggested to be the most susceptible to such mismatching (Saino et al., 2011), and climate change has already been directly linked to the declines of some species (Both et al., 2006a). Climate change also threatens a greater occurrence and variability of extreme weather events, such as reduced rainfall and droughts, specifically on the wintering grounds (Collier et al., 2008; Fauchereau et al., 2003; Nicholson et al., 2000), both of which have been shown to limit several migrant populations (Baillie and Peach, 1992; Blake et al., 1992; Bryant and Jones, 1995; Peach et al., 1995; Szep, 1995a; Winstanley et al., 1974).

Nevertheless, many migrants have shifted the timing of migration in response to changing temperatures (Both and Visser, 2001; Jenni and Kéry, 2003). Some arrive earlier on the breeding grounds in response to increased temperatures in their

wintering quarters, for example (Cotton, 2003). Migration distances have also reduced (Visser et al., 2009). Yet some species may be constrained in how much they can adapt, and those that have not shown a phenological response have shown greater declines than the species that have (Møller et al., 2008). Examples are pied flycatchers, which have advanced their laying dates but not the timing of spring migration, making them susceptible should temperatures change further (Both and Visser, 2001); and common cuckoos, which have failed to advance their arrival dates on the breeding grounds at the same rate as their host species (Saino et al., 2009).

Further anthropogenic drivers

Hunting in southern Europe and North Africa (Berthold, 2001; Böhning-Gaese and Bauer, 1996; McCulloch et al., 1992), increased agricultural intensification in Africa (Söderström et al., 2003), and increasing populations of non-native predators and feral cats (Dauphiné and Cooper, 2009; Loss et al., 2013) most certainly also contribute to migrant declines. Up to 100 million Palearctic migrants are killed annually by hunting in countries that border the Mediterranean (Magnin, 1991), the true consequences of which are largely unknown for almost all species (Baillie and Peach, 1992; Magnin, 1991). Vickery *et al* (2014) list hunting as a likely driver of changes in migrant populations. Some migrant populations have increased under stricter hunting restrictions (Newton, 2004), which suggests that hunting can indeed contribute to declines. Agricultural intensification may also be important. Fertiliser use in Africa trebled and pesticide use increased five-fold between 1970 and 2000 alone (FAOSTAT database of the UN's Food and Agriculture Organisation; http://faostat.fao.org/). Such agricultural intensification is only expected to increase in sub-Saharan Africa, especially since the global food demand is predicted to double over the next 50 years (Tilman et al., 2002; Tilman et al., 2001). Finally, it is estimated that feral cats kill a minimum of one billion songbirds in North America alone (Dauphiné and Cooper, 2009; Loss et al., 2013), likely affecting migrants en route to the wintering grounds in both the New and Old World.

1.8 Optimal migration

As I have argued above, migrants are faced with multitude of additional constraints and considerations compared to non-migratory species, and these constraints and considerations act throughout the annual cycle to influence survival and reproduction. Despite these constraints, the benefits of migration can be maximised in many ways, and similarly there are many solutions to reducing the costs associated with a migratory lifestyle (Delingat et al., 2007). Different strategies exist to optimise body condition, survival and breeding, both between and within species (Catry et al., 2011), such as the intermittent migration of passerines versus the non-stop long-distance flights of shorebirds. Certain general features allow successful migration, as modelled by those exploring optimal migration in detail (Alerstam and Lindström, 1990; Chernetsov et al., 2004; Delingat et al., 2007; Houston, 1998).

Time allocation during migration

Optimal migration demands the optimal allocation of time between each of the migratory stages, such as when to forage or move, when to rest, or when to defend a territory. There is a significant difference between the high-energy costs and no energy income of flight (in-flight starvation), and the high gain and low energy expenditure experienced at stopovers (Bauchinger et al., 2005). How migrants can best to allocate time between moving and resting is therefore crucial for successful migration (Alerstam and Lindström, 1990). Choosing between nocturnal and diurnal flight, for example, is important, because flight should be at times which cannot be best allocated to other activities such as foraging or resting. Time constraints during stopovers force a switch towards optimising rapid mass gain in order to continue migration swiftly. Some species have adopted alternative strategies to intermittent migration to avoid interrupting the migratory journey. Ospreys *Pandion haliaetus* adopt a fly-and-forage strategy, reducing migration time by foraging during migratory flight and still maintain foraging success similar to birds on stopover (Strandberg and Alerstam, 2007). To what extent individuals are constrained by time

throughout migration is likely to be reflected in body condition because of the relationships between fuel load, migration speed and flight distance.

Migrants should be generalists within their wintering habitats

Because of the relatively stochastic and unpredictable nature of migration, being migratory ultimately demands flexibility and the ability to use a wide range of ecological conditions, even if migrants adopt strategies such as being highly site-faithful. Being able to use a wide range of ecological conditions increases both the amount of suitable habitat that is available to migrants and their resilience to changing conditions, allowing them to locate a suitable wintering site sooner and to remain in that site throughout the winter. This lessens the costs of relocating and grants the benefits of being resident. A generalist strategy (defined henceforth as non-specialist requirements within a migrant's wintering habitat) can thus be fundamental to survival when conditions both upon arrival and during winter cannot be predicted.

Furthermore, because constraints and priorities differ between the breeding and wintering grounds and throughout migration itself, being migratory changes whether energy gain and survival must be prioritised over the short or long-term. During the breeding season, breeding adults may prioritise the survival of their offspring over their own long-term survival, yet on the wintering grounds, focus is more likely to shift towards long-term survival, requiring more long-term considerations (Greenberg and Marra, 2005). Being generalist may therefore increase how effectively survival and fitness can be maximised throughout the annual cycle by increasing the range of resources that can be used for energy gain. For example, many migrants are strongly influenced by temporal and spatial variation in resource availability, and must be capable of exploiting resources when they are most abundant or when it is necessary to do so (Alerstam and Lindström, 1990; Bayly, 2007). By having non-specialist requirements within their wintering habitats, migrants are therefore able to utilise a wider range of ecological conditions.

Overall, any increase in survival and fitness granted by adopting a migratory lifestyle can only be realised if the benefits of migrating are maximised and the costs of migration are reduced. Because some species can spend over half of their lifetime migrating, how successfully each stage of migration is optimised can greatly impact both current and future survival and reproduction. But which of the behaviours and strategies discussed may result in optimal migration depends upon the conditions and constraints experienced during migration, and the resulting trade-offs and constraints can carry over to act on other periods in an individual's lifetime. Adopting a migratory lifestyle therefore demands adaptability and flexibility to balance various priorities and constraints, but perfect compensation to changing conditions may not always be possible. Unfavourable or unpredictable conditions en route, temporal and spatial changes in resource availability, available habitat, and predation risk, all demand different optimal solutions. The result is that migrants are pushed from one optimal solution to another in response to changing conditions, and the resulting trade-offs may be optimum but not optimal.

1.9 The wintering ecology of a declining Palearctic migrant

There is little doubt that action is needed to halt and reverse migrant declines; yet even basic information is lacking, especially on the wintering grounds where our knowledge of migrant ecology is poor (Sheehan and Sanderson, 2012; Vickery et al., 2014). As I have argued, which drivers of a decline act on a particular population or species is likely to depend upon aspects of non-breeding ecology, many of which have implications for current and future survival and reproduction and thus population dynamics. Although species vary considerably in their migratory strategies, the similarities are many, and we can probably help direct the conservation of migrant species generally from studying the annual cycle and wintering ecology of even just one species in detail. Here, I therefore explore the influence of the non-breeding season on the population dynamics of a declining long-distance migrant, the whinchat *Saxicola rubetra*, in order to address larger questions about the migration strategies of small passerine migrants and the role of the non-breeding season in migrant population declines.

The whinchat is a small Afro-Palearctic passerine migrant that breeds throughout Europe and western Asia and winters in sub-Saharan Africa, where they are concentrated primarily south of the Sahel in West Africa and in eastern central Africa (Cramp, 1988; Dejaifve, 1994; Elgood et al., 1966; Hagemeijer and Blair, 1997; Pearson, 1972; Urquhart, 2002; Wernham, 2002). Breeding populations have declined drastically in recent decades (Bastian and Bastian, 1996; Callion et al., 1993; Yeatman-Berthelot et al., 1995), with an overall population trend of -16% across Britain in both upland and lowland areas and declines of over 80% in some areas (Gibbons et al., 1993; Henderson et al., 2004). Whinchats are now of conservation concern throughout Europe (Tucker et al., 1994) and are red-listed in some regions, where some populations have been completely eradicated (Burfield et al., 2004; Keller et al., 2001). A principle driver of declines is the loss of breeding habitats, specifically through agricultural intensification and earlier mowing, which causes direct mortality of both nests and adults, reduces food availability, foraging efficiency and fledgling success (Britschgi et al., 2006; Grüebler et al., 2008; Müller et al., 2005; Tome and Denac, 2012).

The role of Africa and the non-breeding season in migrant declines is unclear. Furthermore, population trends vary across European breeding populations, with some showing stable or even increasing trends (BirdLife International, 2014). This suggests that factors other than those acting during the breeding season may influence populations. Recent studies of whinchats wintering in West Africa have suggested that wintering conditions there may not significantly limit populations, and that some human-modified habitats may be beneficial (Hulme and Cresswell, 2012); but studies of this species on the wintering grounds are few. Whinchats are abundant winter visitors to West Africa and are easily observed, making them an ideal model species to study the wintering ecology of Palearctic migrants.

Thesis outline

In this thesis I will test whether whinchats have a generalist migratory and wintering ecology within their wintering habitat of open savannah, as is predicted for most passerine migrants in Africa (Cresswell, 2014):

1. I first address site fidelity and the scale to which whinchats remain in the same area during the winter and return to these areas in subsequent winters, and the scale at which site fidelity can be detected. Knowledge of the scale of site fidelity is important not only for understanding population dynamics and migratory strategies, but also for accurate survival estimates, of which we are lacking.

2. I then explore winter habitat use, the range of habitat characteristics used throughout the winter, the influence that habitat characteristics may have on territory size, and principally which habitat characteristics influence aspects of wintering ecology. I explore age and sex differences and the degree of habitat change throughout winter.

3. Having documented the degree of site fidelity and its implications for survival estimates, I explore both overwinter and annual survival to evaluate where mortality may be occurring throughout the annual cycle. I explore the influence of age and sex on survival and the role of habitat characteristics within territories held in the previous winter.

4. I then present the previously unknown migratory routes, the degree of connectivity and the spatial and temporal aspects of the annual migration cycle of whinchats using geolocators. I describe how migration ecology varies between individuals, and with age and sex, in order to establish both the degree to which whinchats are generalists and any migratory connectivity.

5. Lastly, I will discuss the general implications of the study findings for both whinchats and other Palearctic migrants, such as the degree to which whinchats are winter generalists within their wintering habitat of open savannah, the role the non-breeding season may have in population dynamics, and the conservation implications of our findings.

CHAPTER 2: GENERAL METHODOLOGY

2.1 Study site

This study took place over three consecutive winters (hereby referred to chronologically as winter 1, 2 and 3) from February 2011 to March 2014 on the Jos Plateau in the guinea savannah zone of central Nigeria, West Africa (N09°53', E08°59', approximately 1250 m altitude). The region experiences wet and dry seasons, with the majority of the wintering period for migrants (early September to late April) within the dry season. Study sites were primarily open scrubland with varying degrees of degradation due to habitation, arable farming and livestock grazing, the latter two often increasing in intensity as the dry season progresses (see Hulme and Cresswell, 2012). Sites with high densities of whinchats were chosen and are typical of wintering habitat for this species in the area. Three study sites were used in all winters: site A (open scrub with medium grazing and human activity plus sparse small arable crop fields); site B (open degraded scrub with high grazing and human activity plus small arable crop fields); and site JF (scrubland with light grazing and low human activity plus sparse arable crop fields). Two additional sites were added at the end of the second winter: site H (scrub with light grazing, low human activity and small arable crop fields); and site J (open scrub with heavy grazing and small arable crop fields). Birds were captured at two additional sites in winter 3: site RS (open degraded scrub with arable crop fields), and a site close to site B (open scrub with heavy grazing and some small arable crop fields). See Appendix Figure A.1 for typical images of study sites and changes throughout the wintering season.

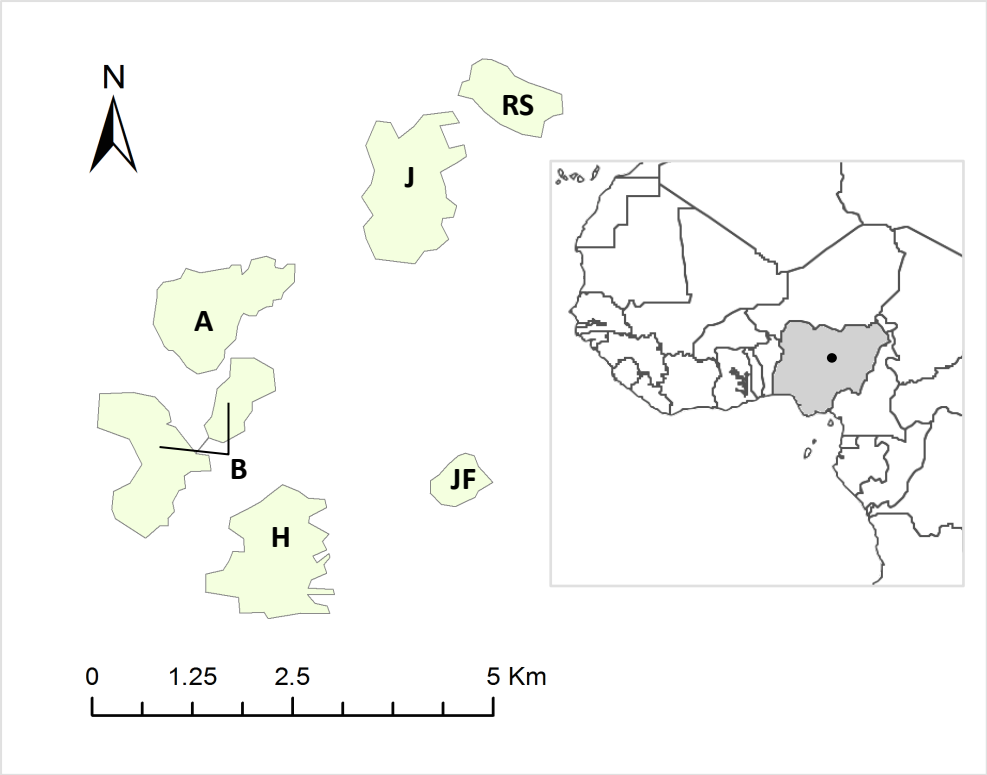


Figure 2.1. Map of the six study sites and location within Nigeria in West Africa. Note that site B is comprised of two adjacent areas.

2.2 Study subjects

Birds were captured with spring traps and mist nets using conspecific playback and live bait. Each bird was uniquely colour ringed, sexed and aged as either first-winter or adult (Jenni and Winkler, 2004), and biometric information (maximum wing cord, tarsus, mass) and moult score recorded. The age and sex of birds caught did not differ between the study sites (Chi squared tests on all birds captured across study: age: $\chi^2 = 2.7$, df = 5, $p = 0.75$, $n = 409$; sex: $\chi^2 = 5.9$, $p = 0.32$, $n = 407$). In total, 458 birds were captured across three winters, of which 334 were resighted at least once after capture, and 179 were fitted with geolocators. 116 birds with geolocators were resighted at least once after capture.

2.3 Resighting individuals

Individuals were resighted throughout winters to determine the location and size of territories (winters 1 and 2), and the degree of residency and site fidelity within and

between winters (all years). In winters 1 and 2, resighting efforts focussed on obtaining undisturbed resightings to gain accurate estimates of territory size and location. In winter 3, resightings were less precise because focus shifted to locating birds. Resightings were carried out from dawn (~06:00) until 11:00 and 16:00 until dusk (~18:30). Whinchats were located with binoculars (Swarovski SV 8x32) and colour combinations read using a spotting scope (Zeiss Diascope 65 mm with 25x eyepiece). Locations of ringed individuals were recorded with a GPS (Garmin GPSMAP 64). To enable unbiased estimates of the territory location, size and use to be determined, each sighting was scored for confidence regarding whether the bird was undisturbed before being sighted, and the date and time to the nearest minute of each resighting recorded. A whinchat could travel across its territory within seconds and the time between observations was found to have no influence on the spatial independence of resightings (General Linear Model of distance between resightings ~ observation time (controlling for individual): $F_{1,762} = 0.02$, $p = 0.90$; 765 observations of 119 individuals). Coordinates were converted to UTM units (Zone 32N) for analyses to give position in metres on the globe. Resightings were viewed and edited where necessary in ArcMAP 10.1 (ERSI, 2012) and Garmin BaseCamp software (version 4.2.4; Garmin International, Inc., Olathe, KS, USA).

2.4 Calculating territory size

The conventional method of determining territory or range size for animals is with Minimum Convex Polygons (MCP), yet this method requires many resightings for accurate descriptions of space use and is subject to several biases (see Börger et al., 2006; Hansteen et al., 1997). Our aim was to determine the area a bird used over winter and the size and location of its territory rather than exact territory boundaries. Therefore we determined an index of territory size from undisturbed resightings for birds resighted in winters 1 and 2. For each individual, the territory centre was determined by averaging the position of all resightings. The mean distance between each resighting and the territory centre was then calculated and doubled to give an estimate of territory diameter that was used as a measure of territory size. Territory size was calculated for individuals with at least five

undisturbed resightings from winters 1 and 2. Five was chosen as a minimum number in order to reduce the influence of increasing resighting sample size on estimates of territory size (Börger et al., 2006), whilst still maintaining adequate sample sizes. Of the 35 and 67 birds resighted in winters 1 and 2, 33 and 39 individuals had at least five independent resightings, respectively. If the minimum number of resightings required to calculate territory size was increased to 10, the average territory diameter was altered by 4 m (6%) and the result of all analyses including territory size were unchanged, suggesting that five resightings were adequate for the following analyses. For birds with territory size indices measured in two winters (i.e. birds ringed in winter 1 and resighted in winters 1 and 2), the average territory diameter was used.

Further methodologies are described in detail within the relevant chapter methods.

CHAPTER 3: HIGH WINTER SITE FIDELITY AND IMPLICATIONS FOR SURVIVAL FOR A LONG-DISTANCE MIGRANT

3.1 Abstract

The decision for a migratory animal to be site faithful in its non-breeding season has profound implications for migratory connectivity, resilience to winter habitat loss and population dynamics through carry-over effects on future breeding success and fitness. Knowledge of the temporal and spatial scale of site fidelity and dispersal is also central to accurate survival estimates. We established the observed spatial and temporal scale of site fidelity within and between years, and determined the ability to detect small-scale dispersal for a declining long-distance Palearctic migrant, the whinchat, on its wintering grounds by comparing predicted and observed detection rates within the study site. Across all years, 54% of individuals returned to the study site and all returning birds reoccupied the same territories they used previously. Observed dispersal was very low even though the probability of detecting any local dispersal was high, suggesting that return rates are indicative of true between-winter survival rates for this population. In any winter, 50% of individuals had a previously occupied but now empty territory that was closer to the centre of their current territory than their average territory diameter; high site fidelity was therefore very unlikely to be because of limited territory availability. Over-winter residency periods differed significantly between individuals and across sites, but residency periods did not determine the probability of returning the next year. This suggests the use of more than one wintering site for some individuals rather than reduced over-winter survival. This study is one of the first to comprehensively document site fidelity at the territory scale in a Palearctic system, although less comprehensive studies or anecdotal evidence suggest high winter site fidelity may be relatively common. Here we provide evidence for the serial residency hypothesis, where selection acts for individual migrants to have non-specialist habitat requirements, allowing them to survive in and remain site faithful to even relatively

low quality, but sufficient and familiar sites. Lower dispersal and higher site fidelity compared to that during breeding suggest that annual survival estimates are more accurate if measured on the wintering grounds.

3.2 Introduction

The non-breeding period is a significant part of the yearly cycle for migrant birds, and wintering ecology has significant carry-over effects for many aspects of survival and reproduction (Baillie and Peach, 1992; Both et al., 2006b; Newton, 2010a, 2006b; Norris et al., 2004; Pulido, 2007; Reudink et al., 2009; Sherry and Holmes, 1996; Studds et al., 2008). A key decision for non-breeding migrants is whether to maintain a winter territory and return to the same wintering site between years, and many migrants have been shown to be site faithful in the non-breeding season to some degree (Cresswell, 2014; Holmes and Sherry, 1992; King and Hutchinson, 2001; Marra, 2000; McNeil, 1982; Salewski et al., 2000; Sauvage et al., 1998). The scale of this site fidelity has substantial consequences for population dynamics and migratory connectivity (Cresswell, 2014; Newton, 2010a), because how dependent a migrant is on specific wintering areas will determine how susceptible (or resilient) that species is to the loss or alteration of those wintering sites. Migrants that are reliant upon few sites are less susceptible to the loss of one or more wintering sites (known as the 'multiple jeopardy' hypothesis (Newton, 2004)).

The more generalist migrants are in their wintering requirements, the greater the amount of suitable habitat that may be available and the greater their ability to stay resident in a territory of poorer quality (Cresswell, 2014). Migrant birds, particularly passerines wintering within Africa, are likely to have generalist (i.e. non-specialist) habitat requirements within their wintering habitats during winter and be faithful to any site that promotes their survival because of the predicted stochastic nature of site selection on a very large scale within the wintering range by birds in their first winter (the serial residency hypothesis – Cresswell, 2014). If wintering sites are lost or change considerably, individuals with a low dependency on specific sites, or those that can use a wider range of winter habitat conditions, can avoid the high costs and

unpredictability of moving long distances, and should have higher survival as a result (Cresswell, 2014; Warkentin and Hernandez, 1996).

At a finer spatial scale, maintaining a territory during the winter as opposed to being itinerant instils knowledge of local food resources and aides territory defence and predator avoidance (Brown and Long, 2007; Förschler et al., 2010). Whether birds occupy a different territory upon return or shift territories within winters can also suggest how important winter territory quality may be for survival and future fitness. Within or between winter territory switching suggests competition for higher quality territories (i.e. dominance-based territory occupancy) and that territory quality influences survival or future reproductive success (Marra and Holmes, 2001). Wintering in sub-optimal habitats has been shown to lower reproductive success for some migrants (Norris et al., 2004; Reudink et al., 2009). This has implications at the population level if habitat loss forces a higher proportion of individuals into lower-quality habitats. Furthermore, if the degree of site fidelity differs with age or sex, any resulting differential survival may lead to skewed population dynamics and related population declines (Marra, 2000; Marra and Holmes, 2001; Sherry and Holmes, 1996; Steifetten and Dale, 2006).

The degree of site fidelity is an essential component of survival estimates, because measuring the scale of site fidelity allows the estimation of “true” survival as opposed to “apparent survival”, the latter of which is a function of the scale and intensity of monitoring and is less valuable for population management (Anders and Marshall, 2005; Ergon and Gardner, 2013; Gilroy et al., 2012; Schaub and Royle, 2013). If migrants exhibit some degree of wintering site fidelity, survival can always be estimated from return rates, at least to some extent (King and Hutchinson, 2001; Salewski et al., 2000; Sauvage et al., 1998); yet determining true survival is problematic because the chance of resighting an individual depends on a combination of survival and dispersal, plus the ability to detect returning individuals (Anders and Marshall, 2005; Marshall et al., 2004; Marshall et al., 2000; Schaub and Royle, 2013). Distinguishing between survival and dispersal is challenging, especially when exploring population dynamics between years (Ergon and Gardner, 2013;

Marshall et al., 2004), and the ability to detect individuals is often a function of the size of the study area and resighting effort (Baker et al., 1995; Marshall et al., 2004; Marshall et al., 2000). Consequently, survival estimates based on return rates often underestimate true survival (Ergon and Gardner, 2013; Gilroy et al., 2012; Schaub and Royle, 2013). Determining where a species lies on the continuum between 100% between-year survival and 100% site fidelity and the degree of any dispersal is therefore fundamental to establishing the value of survival estimates gleaned from return rates. This can be essential to understanding population dynamics. Evidence suggests that fidelity to the same winter territory between years is relatively common amongst migrants (Barshep et al., 2012; Cresswell, 2014; Koronkiewicz et al., 2006; Salewski et al., 2000; Sauvage et al., 1998; Skilleter, 1995), implying that accurate true survival estimates using return rates are indeed possible, although studies of this detail during winter are lacking, particularly for Palearctic migrants (Vickery et al., 2014). Furthermore, accurate between-winter return rates and the temporal scale of within-winter site fidelity are essential to understand whether short-term residency at any one wintering site is due to mortality or dispersal to other wintering sites.

In this study we aimed to establish the degree of site fidelity and quantify the ability to detect any dispersal in a wintering, long-distance Palearctic migrant, the whinchat. This species exhibits varying degrees of fidelity in both the breeding and non-breeding season (Barshep et al., 2012; Bastian, 1992; Shitikov et al., 2012) and has shown significant declines throughout its breeding range over the past few decades (BirdLife International, 2004; Henderson et al., 2004). Declining population trends have been shown for many long-distance Palearctic migrants, the causes of which are often poorly understood (Berthold et al., 1998; Sanderson et al., 2006; Thaxter et al., 2010; Vickery et al., 2014), and so establishing whether migrants are flexible on the wintering grounds and the degree of site fidelity has profound implications for the conservation of migrants. This is particularly relevant given the increasing pressure of anthropogenic habitat loss in Africa (Cresswell, 2014; Warkentin and Hernandez, 1996).

We determine the probability of detecting returning individuals between years, the scale at which both within and between-winter dispersal can be measured, the spatial scale of site fidelity between years, and the temporal scale of site fidelity within years, by addressing the following questions:

1. Do individuals return to the same wintering area and do return rates differ with age and sex?

2. What is the power to detect dispersal and what opportunities are there for individuals to disperse?
   - At what scale can within-winter dispersal be detected?
   - At what scale can between-winter dispersal be detected?
   - What is the power to detect large-scale dispersal?
   - What is the potential for birds to disperse and occupy 'empty' territories upon return?

3. What is the spatial scale of site fidelity and dispersal observed?

4. What is the temporal scale of site fidelity?
   - Are individuals resident within winters?
   - Are there any predictors of residency period?
   - Does the degree of residency over winter predict site fidelity between winters?

3.3 Methods

For details of study sites, resighting protocol, and calculating territory size, refer to Chapter 2: *General methodology*.

Site fidelity

Some individuals that were ringed as juveniles in winter 1 returned in both winters 2 and 3. When calculating return rates, these birds were included as first-winter birds

between winters 1 and 2, and as adults between winters 2 and 3. When modelling predictors of return rates, winter 1 birds returning in multiple years were only considered in return rates between winter 1 to winter 2 to avoid pseudoreplication. To determine the degree of observed site fidelity for winter 1 birds returning in winter 2, we compared the distance between territory centres between years with territory size. Because territory size was not calculated in winter 3 for birds returning from winter 2 due to the less precise resighting methodology, comparing the distances between the mean central point of resighting locations in winter 3 and the mean central point of all available resighting locations in winter 2 established the degree of site fidelity in winter 3.

Establishing resighting effort and detectability

Resighting effort was determined from 94 resighting visits to sites between 1st November 2012 and 24th April 2013 when resighting routes were recorded (note that more resighting visits were made where effort was not recorded but were not when calculating resighting probability). Visits were either partial (<50% of all territories at the site visited) or complete visits (>=50% of all territories visited). A territory was considered visited if the observer walked across an area containing at least 30% of the known territory area. Across all sites, resighting effort was recorded for 33 partial and 25 complete site visits, for which a total number of 82 territories were visited: Site A = 38 total territories: nine complete visits (19-29 territories visited each visit, average 24), 16 partial visits (2-17 territories, average 12). Site B = 25 territories: 10 complete visits (13-22 territories, average 17), 10 partial visits (2-12 territories, average 6). Site JF = 19 territories: six complete visits (10-18 territories, average 14), seven partial visits (3-6 territories, average 4).

Percentage probability of resighting a bird was calculated for individuals recorded at least once during this period as the number times a bird was seen out of the total visits to its territory. The probability of detecting an individual across years, should that individual disperse, was estimated for birds resighted in winter 2 from the proportion of territories that would still be included in the study area in winter 3

after dispersal at increasing spatial scales. Territory diameter was used as territory size. For birds resighted in both winters 1 and 2, territory diameter from winter 2 was used. For birds where the territory location was known but territory diameter not calculated due to an insufficient number of resightings (n = 52 birds), we used the mean territory diameter across all individuals. A GIS was used to determine detection probability after dispersal (ArcMAP 10.1 (ERSI, 2012)). To do this, possible territory locations were determined using a combination of the Buffer tool (to create new territories of multiples of the territory size for each individual) and the Union feature in the Overlay Analysis Toolbox to calculate the location of territories after dispersal and the proportion still within the study area.

Within-winter residency period

There was a negative relationship between capture date and residency period if individual residency period was calculated as the period from capture date to last resighting (b = -1.22, t_{55} = -2.9, R^2 = 0.12, $F_{1,53}$ = 8.5, p <0.01): i.e. birds caught late in the year could only be resident for shorter periods). This meant that capture date could not be used as a biologically meaningful predictor of how long whinchats chose to spend in a wintering territory. Consequently, residency time was defined for each individual as the number of days from the middle of the catching period (22nd October) until the last resighting for that individual. Individual capture date could then be used as a simple predictor of residency period with last resighting day included in the model as a representation of departure date.

Sample sizes and statistical analyses

Birds were only included in the study if resighted at least once after capture. Birds from sites A, B and JF are included in all analyses, whereas birds from sites H and J were excluded from analyses involving territory size because only approximate locations (and not undisturbed resightings as required for accurate territory estimates; see Chapter 2: *General methodology*) were recorded for these individuals. One individual was excluded from analyses exploring probability of detection

because its territory was visited too infrequently. Birds which could not be confidently aged or sexed were excluded from models including age and sex as predictors. The numbers of individuals included in this study are shown in Table 3.1.

Table 3.1. Numbers of birds involved in the study each year which were resighted at least once and known to be resident, separated by winter and age. Figures show numbers of individuals, with percentages in brackets. Birds ringed as first-winter birds are included in adult totals for subsequent years if they returned after their ringing year. Birds of unknown age (winter 1 *n* = 1, winter 2 *n* = 2) are excluded from age-specific totals but are shown in brackets in the study total column. In four cases (two in winter 1 and two in winter 2) a bird was only resighted after capture in the following winter.

	First-winter	Adult	Study total (+U age)
Winter 1	12 (33%)	24 (67%)	36 (1)
Winter 2	33 (40%)	49 (60%)	80 (2)
Winter 3	48 (34%)	94 (66%)	142 (0)
Total			195 (3)

Aspects of wintering ecology were explored with General Linear Models carried out in R version 3.0.1 (R Development Core Team, 2013) and RStudio Version 0.98.507. Analysis of Variance (ANOVA) was used to explore differences in resighting probability across sites. Generalised Linear Models (logistic regression) was used for exploring predictors of return rates and the influence of residency period on the probability of return in the following winter. To determine whether short residency periods were due to mortality, return rates for the following winter were compared between individuals that left sites early (short residency period) and those that remained for at least 50% of the winter (long residency period). General Linear Models were used to explore predictors of residency period. Paired *t*-tests were used to explore differences in territory size between years. Multiple regression model simplification was based on Akaike Information Criterion (AIC) (Bozdogan, 1987), where variables failing to improve AICc (within two AICc of the top model) or add a significant contribution to the model (as determined by a non-significant

ANOVA comparison between models) were removed from the model. For models of the same or similar sample size, dredge analysis was used to identify minimal adequate models (Bartoń, 2012): cases with missing values were removed from the dataset as required for dredge analyses, and resulting minimal adequate models were produced using complete datasets. When presenting top models from dredge analyses, we presented models within two, three or four AICc of the top model based on which value gave a representative number of top models. Model fits were evaluated from diagnostic model plots and models presented if assumptions were reasonably met (Crawley, 2007). Data were checked for normality when necessary and for multicollinearity with variance inflation factors in the CARS package (Fox and Weisberg, 2010). Mean values are presented as means ± one standard error in all cases. A statistical significance level of p <0.05 was chosen to reject null hypotheses.

3.4 Results

1. Return rates to the study site and influence of age and sex

Return rates were 58% in winter 2 and 52% in winter 3, averaging 54% across the two winters. In no cases did a bird fail to return in its second winter but then return in its third winter. A bird's age or sex did not influence the probability of resighting that individual in the following winter (Logistic regression: model averaged parameters of top 11 models within four AICc ranks of the top model: age: z = 0.7, p = 0.47; sex: z = 0.04, p = 0.97; body size at time of capture, winter and site also included within main model (all terms including interaction terms between age, sex and site not significant)).

2. Power to detect dispersal and opportunity for dispersal

Probability of detection within winters

Across all individuals, the probability of resighting an individual that was seen at least once after ringing if its territory was visited once was 63% (±2.4%, range 11 –

100%, *n* = 81). Each time a site was visited, 59% of birds on average were detected out of all birds whose territories were visited (±3.3%, range 0 – 100% detected, *n* = 77). On average, each territory was visited nine times during the study period for which resighting effort was known (±0.51, range 1 – 18, *n* = 81). When accounting for the probability of encountering a bird when its territory was visited, there was a probability of almost 100% of detecting a resident individual during a study winter.

The probability of resighting an individual did not vary between sites (F_2 = 2.6, *p* = 0.08, *n* = 81), nor with the number of days into the study ($F_{1,78}$ = 0.5, β = -0.24, SE = 0.33, R^2 = -0.06, *p* = 0.47, *n* = 81; Figure 3.1a). Similarly, the proportions of individuals resighted each visit did not differ between sites ($F_{2,74}$ = 0.5, *p* = 0.63, *n* = 77), nor with number of days into the study ($F_{1,75}$ = 0.6, β = 0.00074, SE = 0.00095, R^2 = -0.005, *p* = 0.44, *n* = 77; Figure 3.1b).

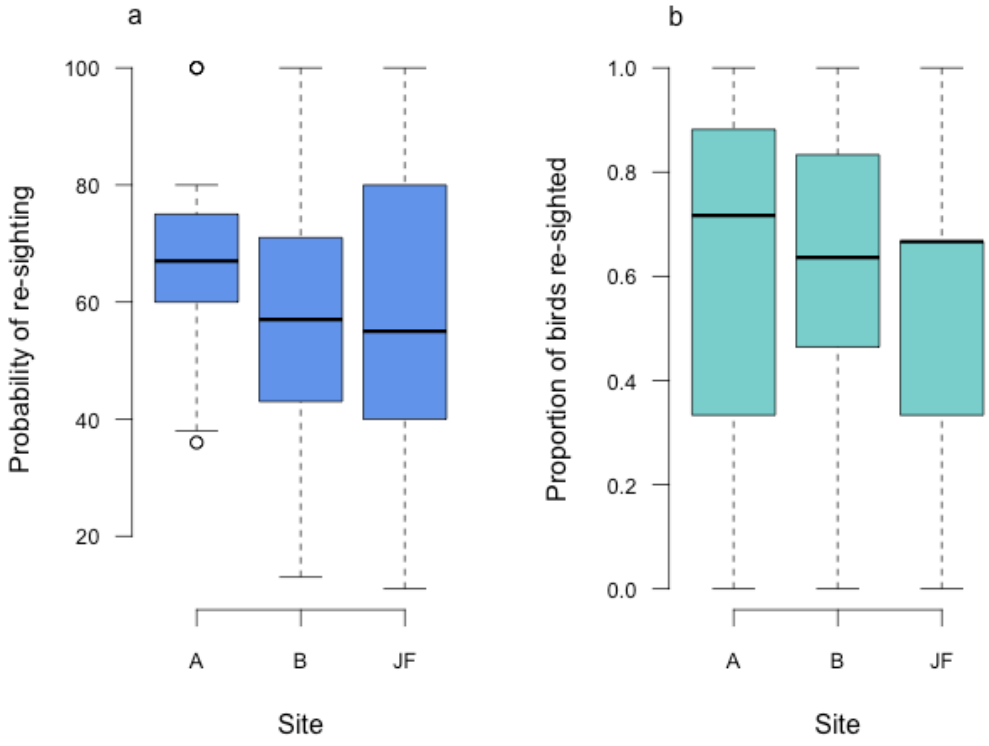


Figure 3.1. a) The percentage chance of resighting a bird if its territory was visited, and **b)** the proportion of birds resighted out of the number of territories visited during a site visit, across the three study sites. There was no difference in the probability of seeing a bird or in the proportion of birds detected during visits across sites.

Probability of detecting dispersal between years

On average, a bird could have dispersed up to eight territories when returning in the subsequent year (representing a mean distance of 545 m across all territories measured, *n* = 130) before the chance of it remaining within the study area dropped below 50% (mean proportion of the territory within the study area after eight territory shifts = 47% (±2.1%), range 0 – 95%, *n* = 130; average territory diameter across all birds in both years was 64 m (±1.8 m), range 11 – 106 m, *n* = 113 (Figure 3.2)). On average, the probability of a bird remaining in the study area reduced by 7% if it moved by one full territory. 60% of all birds had at least a 50% probability of remaining in the study area after dispersing seven full territories, with 25% of birds (*n* = 32) maintaining a probability of occurrence in the study area of at least 80% if they shifted as many as six territories (Figure 3.2). A 500 m shift from the territory location in the previous year (for birds resighted in winter 2) resulted in a 44% probability of staying in the study (±1.9%, range 0 – 86%, *n* = 132). On a larger scale, the probability of staying in the study area was 16% for a territory shift of 1 km (±0.8%, range 0 – 36%, *n* = 132) and 2% for a shift of 5 km (0.2%, range 0 – 7%, *n* = 132). No birds would have been within the study area if they dispersed 10 km or more in the following year.

Overall power of estimating larger-scale dispersal

Overall, 89 individuals were known to be resident in winter 2 (of a total of 132 but 43 individuals fitted with geolocators were excluded). With observed return rates of 54% and site fidelity at the territory level, 48 individuals returned to their territories in the following year. Of the remaining 41 individuals, assuming all survived, eight, four and two birds should have been found within the study site if they dispersed 0.5 km, 1 km or 5 km respectively (Figure 3.3). If only 50% (*n* = 20) of these individuals had survived and dispersed, four, two and one birds respectively should have been detected away from their territories.

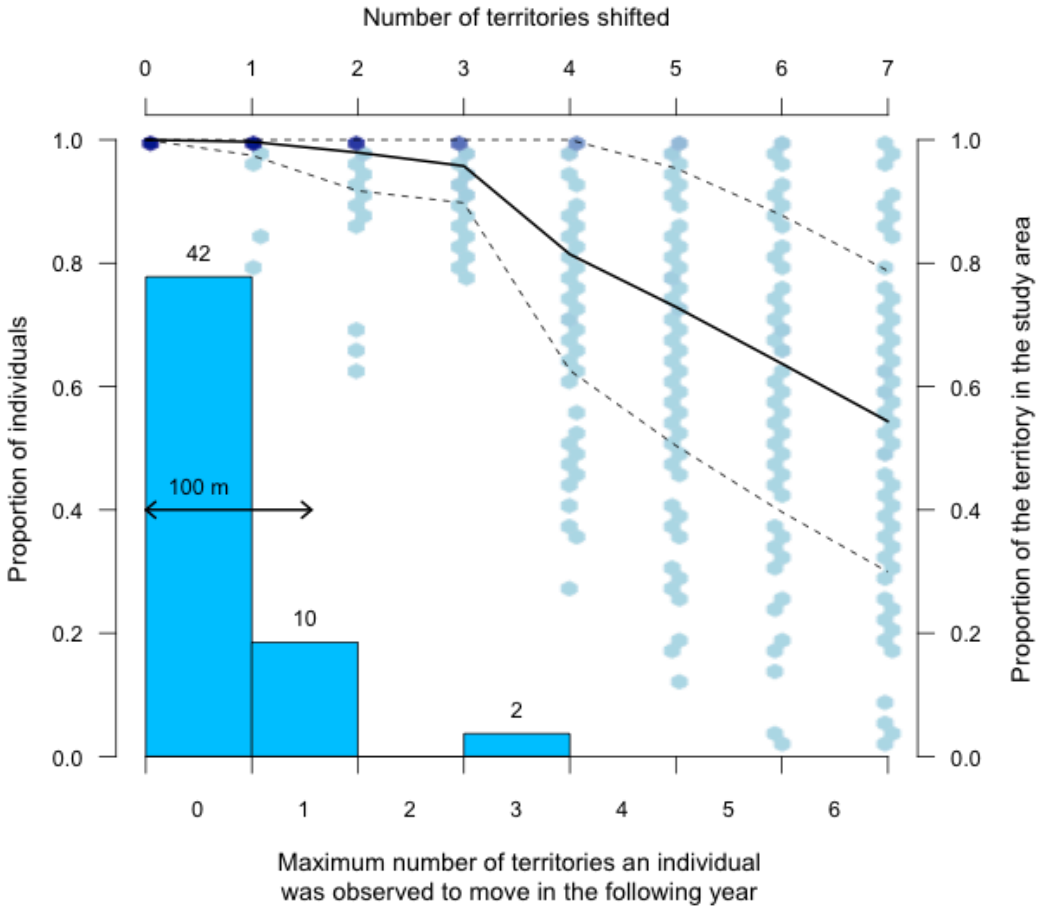


Figure 3.2. The probability of detecting a returning bird within the study site in the following year if small scale dispersal occurred from the territory location in the previous year (◆, as determined by the proportion of the study area that could contain the territory after dispersal), and the maximum distance individuals were actually observed to move the following year (blue bars; *n* = 54). The shade of each point represents the frequency of individuals with that value, where darker shades represent higher frequencies, starting from dark blue (furthest left data point). The mean proportion of the new territory within the study area should dispersal occur is also shown (solid black line) with upper and lower CIs (dashed lines).

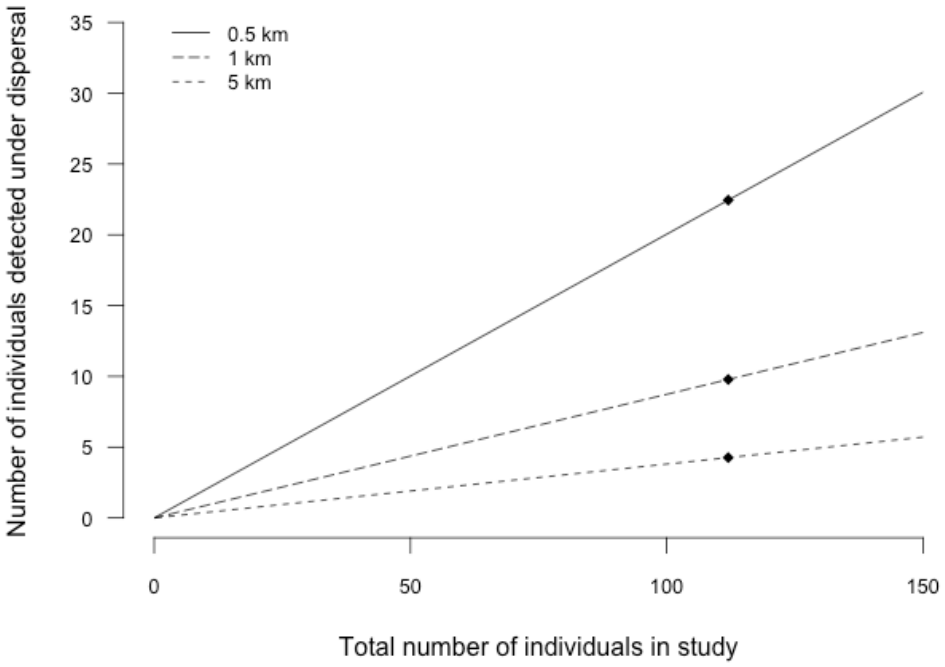


Figure 3.3. The number of birds estimated to be within the study area if dispersal occurred of 0.5 km, 1 km and 5 km upon return to the study site the following winter assuming a return rate of 54%, as a function of the total number of birds studied in a year. The actual number of individuals studied – i.e. where territory diameter was measured – is also shown (◆; *n* = 112).

Opportunity for local dispersal

For returning birds, the average distance between the territory centre in the first year and the centre of the nearest unoccupied territory (i.e. a territory that was occupied in the previous winter but now empty) in the following year was 107 m (±10.0 m, range 7 – 538 m, *n* = 76, Figure 3.4). On average, each individual had at least one known unoccupied territory within 100 m, and three unoccupied territories within 200 m of the centre of the territory in the previous year (*n* = 80). For birds for which the location of the territory centre was accurately known in both years, 50% of individuals had unoccupied territories that were closer to the territory centre than their average territory diameter (*n* = 19).

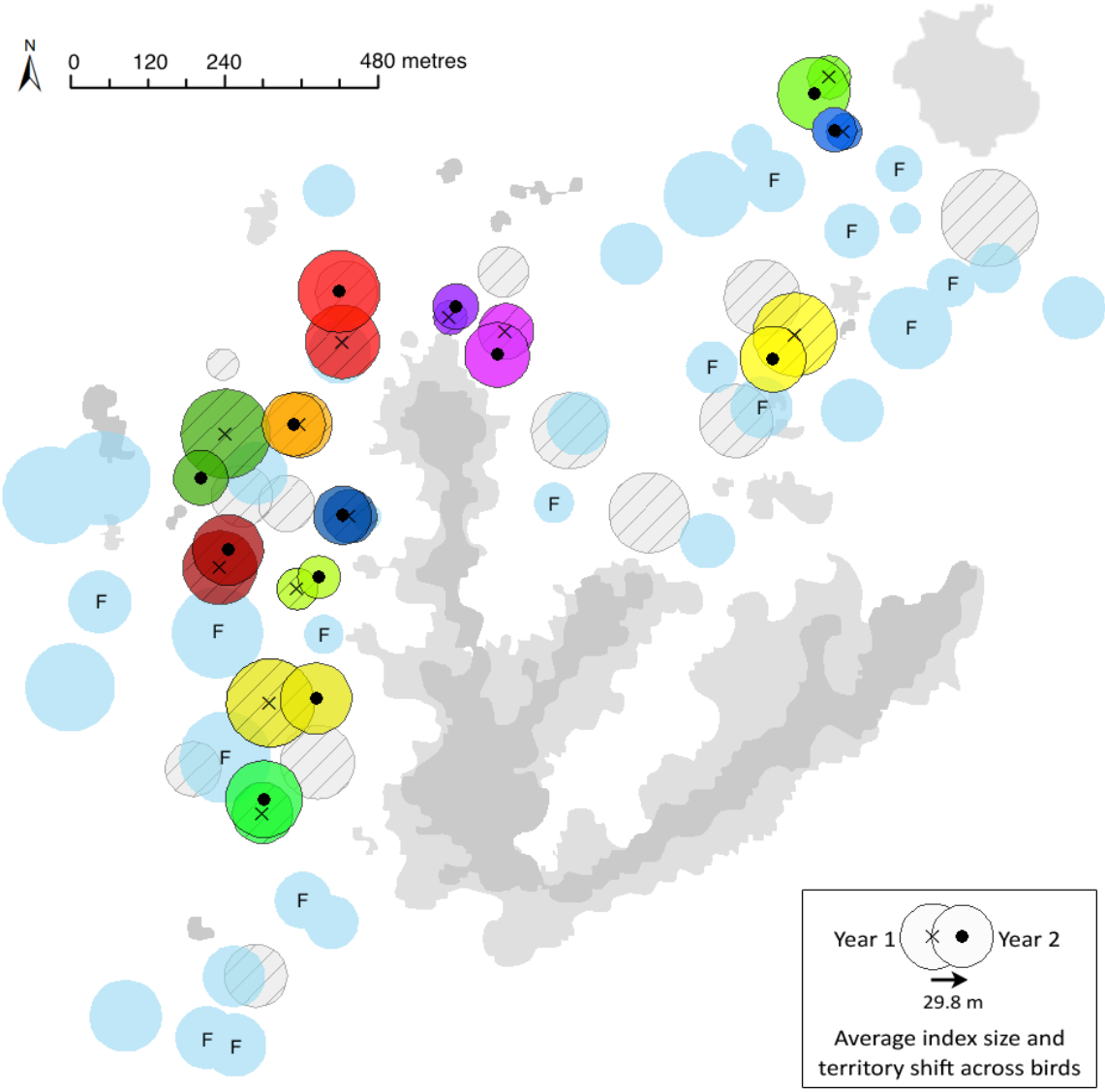


Figure 3.4. Map of study site A showing territories of birds that returned in winter 2 (plain coloured circles with • symbol) relative to territories held by the same birds in winter 1 (coloured hashed circles of the same colour with **x** symbol). Each circle represents a whinchat territory in either winter 1 or winter 2, the radius of which is equal to the individual's index of territory size (m). Territories sharing the same colour belong to the same returning individual in winter 1 and winter 2, excluding a) hashed grey circles, which show territories of birds ringed in winter 1 that failed to return to the study site in winter 2, and b) plain light blue circles, which show territories of birds newly ringed in winter 2 where an F indicates a first-winter bird (note this does not necessarily mean that these territories were unoccupied in winter 1). Solid grey areas show areas of thick scrub. All of a) and those territories of b) occupied by first year birds

represent territories available to returning birds. The inset figure shows the average territory size in each winter and the average distance between territories of a returning individual in winters 1 and 2. Overall the figure shows that each bird returning to the study area returned to the same territory used in the previous year despite many empty territories being available close by.

3. Scale of spatial site fidelity and levels of dispersal detected

Winter 1 vs. winter 2

The average movement between territory centres in winter 1 vs. winter 2 was 30 m (±4.0 m, range = 6 – 58 m, *n* = 19; Figure 3.4). The furthest movement was 58.3 m. For all individuals, any movement in the centre of the territory between years was less than the territory size for that individual in winter 1 (average difference between movement across years and territory size in winter 1 = -35.5 ±3.4 m, range = -61 – -2 m; Figure 3.4), showing that individuals returned to the same territory in winter 2 and that "movements" observed were likely due to the resolution at which data were collected rather than actual territory shifts.

Birds returning from winter 1 used statistically the same sized territory in winter 2 (paired *t*-test: $t = -0.07$, df = 17, $p = 0.95$, $n = 18$; Figure 3.4).

Winter 2 vs. winter 3

Across all individuals, birds were resighted on average 21 m from where they were seen in the previous year (±3.2 m, range = 1 – 118 m, *n* = 54) and none were resighted further than 118 m from any one known location in the previous year. In terms of range size, the average difference between the maximum range in winter 2 (as determined by the furthest distance between known locations) and the distance between the furthest resighting in winter 3 from a known location in winter 2 was 55 m (±5.5 m, range = 2 – 165 m), equal to less than the width of one territory (Figure 3.2).

4. Temporal scale of fidelity

Degree of residency and predictors of residency period

Residency periods varied widely across individuals, from 25 to 211 days (mean 85.2 ±6.0 days, *n* = 55; Figure 3.5). Residency periods differed significantly according to age and also differed across sites, with birds spending less of the winter at site JF relative to site A. (Table 3.2; Figure 3.6). There was also a significant interaction between site and age, where residency time was significantly shorter for adults than first-winter birds at site A, but similar at sites B and JF (Figure 3.6)

Relationships between residency period and probability of return

Nineteen of 33 birds with short residency periods and 11 of 22 birds with long residency periods returned the following winter (*n* = 55; Figure 3.5). Return rates did not differ between birds with short or long residency periods (Logistic regression: z = 0.6, Residual deviance (53) = 75.45, p = 0.58, AIC = 79.5, *n* = 55), nor according to last resighting day or between sites (Table 3.3; Figure 3.5); i.e. birds which were resighted for only a short duration of the winter were just as likely to return in the following winter as birds that were resident for most of the winter.

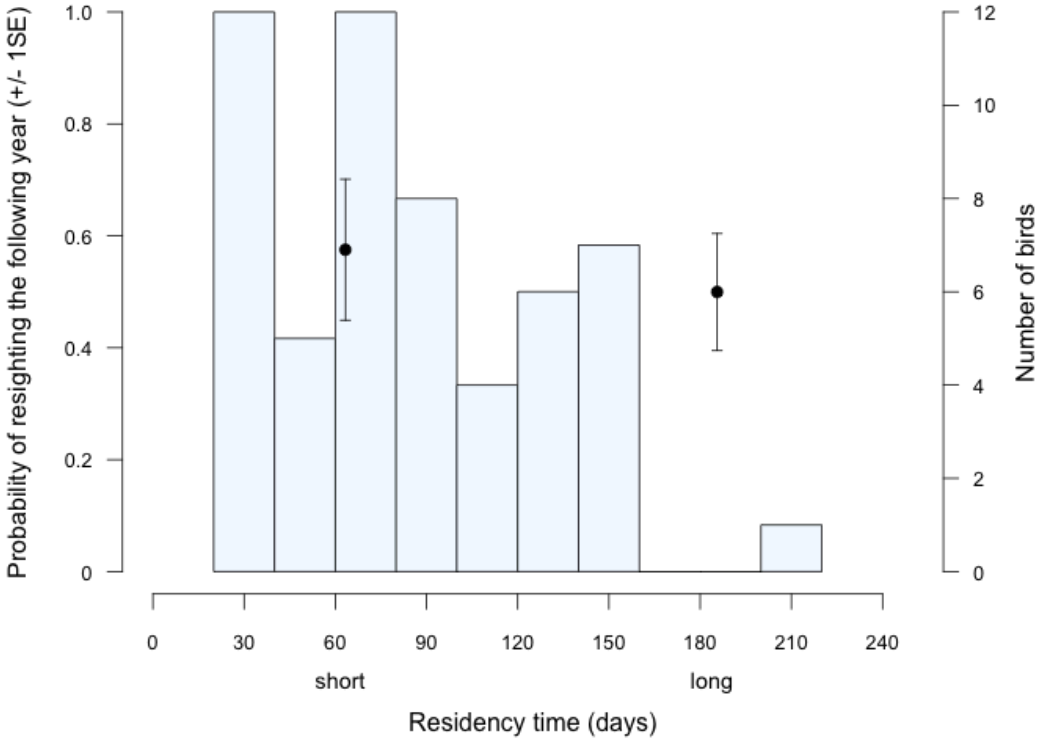


Figure 3.5. Residency times of whinchats (number of days since mean capture date until last resighting; blue bars) plus predicted values for probability of return in following winter according to residency period (short or long, as defined as being present or absent after the middle of the wintering period) in the previous winter (±SE; black circles with error bars) from a logistic regression analysis of return ~ residency period (see Table 3.3). Residency time had no significant influence on the probability of return (*n* = 55).

Table 3.2. Results from General Linear Models exploring predictors of residency period. The first model (initial maximal model of: residency period since average capture date ~ age + sex + site + capture day + age*site + sex*site, *n* = 53) is presented as the results from averaging the top four models (within 4 AICc of the top model), along with the top model. Residual SE for top model = 29.3 on 47 df; multiple R-squared = 0.61; $F_{5,47}$ = 14.7; overall *p*-value = <0.0001, *n* = 53. Note that site A and age = adult are the reference categories. Significant terms are shown in bold.

	Full model		All models ΔAIC < 4			Top model			
Variable	*z*	*p*	Model-averaged parameter estimate	SE	Relative weight	Parameter estimate	SE	*t*	*p*
(Intercept)	5.3	**<0.001**	103.1	15.1		99.1	11.1	9.0	**<0.001**
Age FW	2.8	**0.049**	34.6	17.2	1.00	47.4	14.4	3.3	**0.0019**
Site B	0.6	0.074	-28.7	15.8	1.00	-18.2	13.6	-1.4	0.19
Site JF	2.9	**<0.001**	-72.8	16.5		-64.0	16.3	-3.9	**<0.001**
Age F:site B	2.5	**0.035**	-43.3	20.0	0.47	-45.0	19.4	-2.3	**0.025**
Age F:site JF	1.8	0.18	-30.6	21.6		-30.7	21.4	-1.4	0.16
Sex M	1.0	0.23	11.3	9.1	0.36				
Capture day	0.7	0.88	0.01	0.3	0.18				

All interaction terms between age, sex and winter NS

Table 3.3. Results from logistic regression analyses exploring the influence of residency period on the probability of return in the following year, from the initial maximal model of: returned next year ~ last resighting day + residency time + site + residency time*site. The full model is presented as the results from averaging the top five models (within 4 AICc of the top model). The Null model was the top model (all terms NS, Residual deviance for full model = 73.1 on 50 df; AIC = 83.1). Note that site A and long residency time are the reference categories; *n* = 55.

Variable	SE	*z*	*p*
(Intercept)	2.70	0.6	0.57
Last resighting day	0.01	-0.5	0.62
Residency time (short)	1.05	0.4	0.68
Site B	0.83	-0.7	0.50
Site JF	1.12	-1.4	0.17

All interaction terms between residency time and site NS

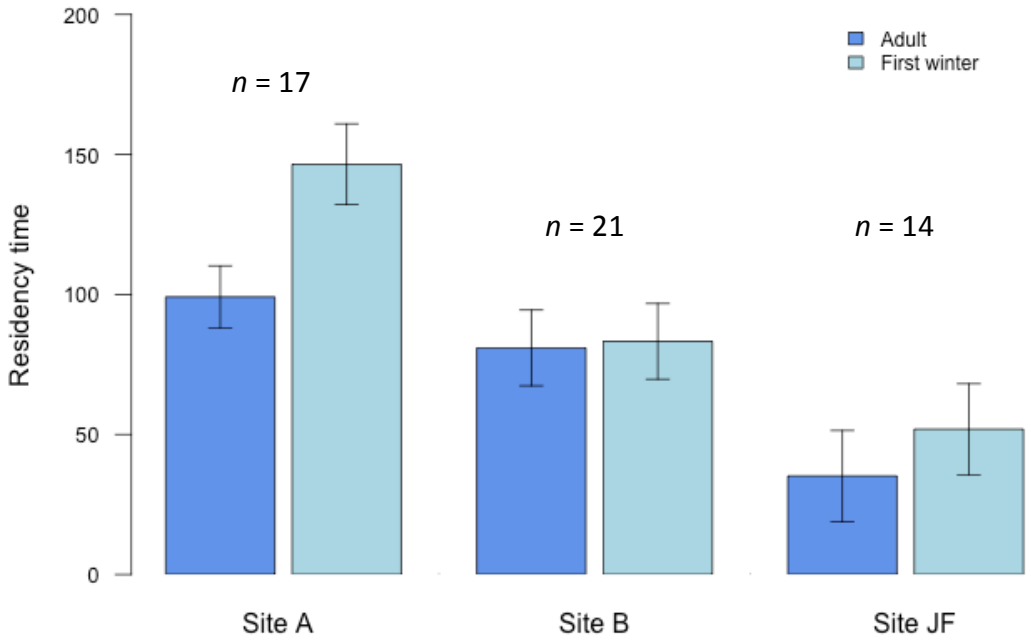


Figure 3.6. The difference in mean time spent resident at each site between adult and first-winter birds. Values are predicted from the model residency time ~ site + age + site*age (Table 3.2, *n* = 55). Residency periods differed significantly across sites. First-winter birds also remained resident for significantly longer periods at site A relative to sites B and JF.

3.5 Discussion

Return rates, dispersal and the ability to estimate 'true' survival

The lack of local dispersal and low probability of large-scale dispersal suggests that a return rate of 54% across the study closely mirrors true between-winter survival for whinchats. Although we are not aware of any other studies documenting between-winter return rates or survival for this species on the wintering grounds, our return rates in both years are similar to or are higher than return or survival rates documented for whinchats and other site-faithful Palearctic migrants on the breeding grounds (whinchat: return rates of 11 – 47% (Bastian, 1992; Bezzel and Stiel, 1977; Schmidt and Hantge, 1954); great reed warbler *Acrocephalus arundinaceus*: return rate of 55% (Bensch and Hasselquist, 1991); barn swallow *Hirundo rustica*: survival estimates of 0.36 – 0.42 (Møller and Szép, 2005; Robinson et al., 2008); sand martin *Riparia riparia*: survival estimates of 0.29 – 0.31 (Cowley and Siriwardena, 2005; Robinson et al., 2008); common house martin *Delichon urbicum*: survival estimate of 0.42 (Robinson et al., 2008), and also many Neotropical migrants (Desante et al., 1995). This is not surprising, given the high site fidelity we documented and our ability to detect dispersal on the wintering grounds. If this is generally true across migrants, annual survival estimates from the wintering grounds are likely to be more accurate than those estimated on the breeding grounds, almost certainly because of the higher breeding dispersal often reported. Consequently, our results suggest that studies aiming to accurately measure annual survival for migrants should focus on winter return rates.

Because of our ability to detect any dispersal occurring on a number of scales, we are confident that our findings of extremely high site fidelity are a true representation of wintering behaviour. There was a high probability of encountering locally dispersing birds – at least 50% of 'missing' individuals would have been detected if they had dispersed up to eight territories upon return and nine individuals would have been detected if they moved 0.5km – yet observed dispersal was extremely low. When we were able to compare territory locations between

years, all individuals returned to the same territory they held in the previous winter and no bird was resighted more than 118 m from where it had been seen in the previous year. Therefore, if dispersal did occur, this was only on a larger scale (i.e. greater than 5 km). As we did not have the ability to detect any movements of this scale we cannot rule out that this population could be comprised of both highly resident and widely dispersing individuals. However, the similarity between observed return rates and those expected when comparing studies of other migrants and return rates on the breeding grounds (see above) plus extremely high site fidelity at the territory-scale implies that any large-scale dispersal was unlikely.

Site fidelity and wintering strategy

To our knowledge, this is one of the first studies to document site fidelity at a large and fine scale for a Palearctic migrant on the wintering grounds and to further explore the influence of local dispersal on such findings. Our results support previous observations that whinchats are site faithful (Barshep et al., 2012), but at a much finer scale than originally thought. Birds returned to the same territory, and within-winter fidelity was high because birds held small, distinct territories whilst resident. Repeat occupancy of winter territories has been documented in several other migrants, including whinchats (Cuadrado, 1992; Dejaifve, 1994; Holmes and Sherry, 1992; Holmes et al., 1989; Kelsey, 1989; Koronkiewicz et al., 2006; Kricher and Davis, 1986; Marra, 2000; Salewski et al., 2000; Sauvage et al., 1998; Skilleter, 1995), along with territoriality over winter (Bates, 1992; Brown et al., 2000; Kelsey, 1989; Latta and Faaborg, 2001; Rappole et al., 2003; Salewski et al., 2002a), indicating that high site fidelity may be relatively common across long-distance migrants.

Our findings suggest that the benefits of winter territoriality and site fidelity outweigh the benefits of competing for or moving to higher quality territories during winter. High site fidelity most likely results in site familiarity, likely greater predictability of foraging opportunities, and more efficient territory defence and predator avoidance, all of which will promote survival (Brown and Long, 2007; Förschler et al., 2010). Moving or not holding a winter territory, on the other hand, is

often associated with reduced survival (Rappole et al., 1989; Winker, 1998). Furthermore, the benefits of high site fidelity both within and between years may be greater during winter than during the breeding season because the potential benefits of dispersing to find a mate or a suitable nesting location are absent. Site fidelity on the breeding grounds is often lower than winter, even if a species shows high site fidelity on the wintering grounds (Herremans et al., 1995; Koronkiewicz et al., 2006; Tryjanowski et al., 2007). Evidence suggests that this may also be true for whinchats (Bastian, 1992; Bezzel and Stiel, 1977; Shitikov et al., 2012), with territory fidelity often reported to be lower for whinchats on their breeding grounds than what we document here for winter (Bastian, 1992 and references therein; I. Henderson and J. Taylor, unpublished data). Most likely, the additional pressure of mate acquisition reduces any benefits of very high fidelity at the territory-scale on the breeding grounds because both individuals would have to survive if either is to breed, and dispersal is also required to prevent inbreeding. Breeding site fidelity may therefore only benefit individuals if it occurs at a larger scale, such as fidelity to a larger breeding region. In agreement with this, marsh warblers *Acrocephalus palustris* have been shown to hold territories for longer periods in winter than in summer, for example, suggesting that winter territoriality aids the defence of long-term resources (food availability) rather than short-term resources (breeding partners) (Kelsey, 1989). In short: there may be many reasons that force a breeding bird to move – death or movement of a partner, lack of nesting habitat, lack of resources to raise chicks etc. – while a wintering bird requires only a relatively low level of resources to ensure daily survival and therefore has fewer reasons to move.

High site fidelity, especially within winters, should demand a non-specialist wintering strategy so that survival and future reproduction is not significantly influenced by fine-scale variation in territory characteristics. As conditions often alter during winter (see Chapter 4: *Winter habitat*), territoriality demands that a wide range of conditions can be utilised. For example, Salewski et al. (2002) hypothesised that winter territoriality in pied flycatchers *Ficedula hypoleuca* was a result of a more diverse and generalist foraging strategy, enabling individuals to reside in and defend

small areas over the winter. Other migrant species have indeed suggested to be winter generalists (Latta and Faaborg, 2002).

Our results indicate a lack of dominance-based territory occupancy during winter, suggesting that individual whinchats do not compete much, if at all, for territories of higher quality. Returning whinchats always returned to the same winter territory, regardless of the proximity of an alternative territory. Because the costs of moving very short distances are likely to be low and at least some available territories are likely to be of higher quality (if summer mortality is indeed largely independent of winter territory quality), individuals must not have benefited much from moving between territories. This suggests that territories do not differ greatly regarding their influence on survival, or that whinchats have few wintering requirements. Consequently, variation in winter territory habitat characteristics is unlikely to have large carry-over effects on future survival and breeding success, and a 'good' winter territory is simply one that promotes survival. Likely, winter territories have little influence on the success of migration. Whinchats may be able to fatten for migration in a range of conditions, even sub-optimal, or may have additional stopover sites between leaving the winter territory and crossing the Sahara specifically for fattening. The fact that whinchats occupy and defend a winter territory shows that some form of competition occurs on the wintering grounds; however this is likely to be for the defence of a familiar and predictable resource rather than competition related to variation in those resources.

The additional benefits of enhanced local knowledge and predictability that site fidelity brings should further encourage individuals to be site faithful at such a small spatial scale. In contrast, higher territory fidelity has been shown for adults over first years and males over females for whinchats on the breeding grounds, along with higher return rates for adults over first years (Bastian, 1992 and references therein). On the wintering grounds, dominance-based winter habitat occupancy has been documented for red-backed shrikes *Lanius collurio* (Herremans, 1997), Eastern great reed warblers *Acrocephalus orientalis* (Nisbet and Medway, 1972) and European robins *Erithacus rubetra* (Catry et al., 2004a), and for many Neotropical migrants,

such as American redstarts *Setophaga ruticilla* (Marra, 2000; Marra and Holmes, 2001), prairie warblers *Setophaga discolour* (Latta and Faaborg, 2001), hooded warblers *Setophaga citrina* (Lynch et al., 1985; Morton, 1990; Stutchbury, 1994) and black-throated blue warblers *Setophaga caerulescens* (Wunderle Jr, 1995), amongst others (Ornat and Greenberg, 1990).

Difference in residency times

Whinchats were resident at winter sites for 85 days on average, although there was large variation across individuals. Only residency period and not the degree of territoriality (i.e. age or sex-specific variation in the degree of territory defence) varied across sites, as also shown in wintering pied flycatchers (Salewski et al., 2002a). The probability of returning in the following winter did not differ with residency time, suggesting that some individuals may have multiple wintering sites. Multiple site use by individuals has been described in several migrants in both the Neotropical and Palearctic system (McKinnon et al., 2013a), and some migrants may move southward during the winter (Cresswell et al., 2009), possibly in response to changing conditions (Jones, 1995). The early departure of these individuals may provide territories for winter floaters, the presence of which is suggested in some studies (Winker, 1998) when birds that disappear during winter are replaced by new individuals (Brown and Long, 2007; Holmes et al., 1989; Morton et al., 1987). Further studies involving immediate ringing of individuals at a site regardless of territory occupancy and very high-effort resighting would be needed to establish whether winter floaters are indeed present in this wintering population. Observations made during this study suggest that whilst some empty territories were reoccupied, others remained empty for the remainder of the winter, even though they had been used previously. Because individuals do not appear to compete for territories of varying quality, do not move even when given the opportunity, and likely have non-specialist wintering requirements, most likely winter territories are plentiful, and therefore not all suitable territories are occupied.

In summary, we documented extremely high site fidelity by individuals both between and within-winters and a lack of dominance-based territory occupancy in a long-distance migrant. We provide strong evidence for a generalist wintering strategy within open savannah and evidence that winter territory quality may have little influence on future survival and breeding success. This study supports the serial residency hypothesis (Cresswell, 2014), where selection acts for most migrants to have generalist habitat requirements, allowing them to survive in and remain faithful to even relatively low quality, but adequate and familiar sites. Due to lower dispersal and higher site fidelity during winter compared to breeding, the ability to accurately measure annual survival rates may be highest on the wintering grounds. Furthermore, generalist wintering requirements and the seemingly high availability of suitable wintering territories may provide some resilience to the on-going habitat degradation occurring throughout Africa.

CHAPTER 4. GENERALIST WINTER HABITAT REQUIREMENTS FOR A DECLINING OVER-WINTERING MIGRANT: EVIDENCE FOR THE SERIAL RESIDENCY HYPOTHESES

4.1 Abstract

For migrant birds, the degree of habitat specialism and whether dominance-based habitat occupancy occurs during the non-breeding season directly influences migration ecology, future survival and breeding success. Because site selection within the wintering range is likely stochastic during the first migration and wintering conditions are unpredictable (the serial residency hypothesis), increasing the scope of habitats that can be used increases habitat availability and population resilience to habitat loss. We tested to what degree and at what scale a declining Palearctic migrant, the whinchat, is a winter habitat generalist within open savannah. We explored the influence of habitat characteristics at the territory-scale and whether dominance-based habitat occupancy occured by describing the variation in habitat characteristics across wintering territories, the degree of habitat change within territories held throughout winter, and whether habitat characteristics influenced territory size and space use or differed with age and sex. A typical territory had some grazing, human disturbance and farmed land. Habitat characteristics varied across territories and birds maintained their territories even though habitat changed significantly throughout winter. We found no evidence of dominance-based habitat occupancy; instead, territories were smaller if they contained more perching shrubs or maize crops, and areas within territories with more perching shrubs were used more often, likely because perches are important for foraging and territory defence. Our results suggest that whinchats have non-specialist winter habitat requirements and respond to habitat variation by adjusting territory size and space use within territories, rather that by competing with conspecifics for territories of varying quality, and support previous findings that some crop types may provide high-quality wintering habitat by increasing perch density. By being winter generalists, migrants are likely to be flexible to changing wintering conditions in Africa, both within and

across winters, so possibly engendering some resilience to the rapid anthropogenic habitat degradation occurring there.

4.2 Introduction

For migrant species, conditions in both the breeding and non-breeding season have a strong influence on life history traits and therefore population dynamics (Moore et al., 1995; Newton, 2010a). Habitat selection during winter influences many aspects of migration and subsequent breeding ecology, with consequences at both the individual and population level (Newton, 2010a; Sherry and Holmes, 1996). Principally, conditions over winter affect body condition (Ottosson et al., 2005; Strong and Sherry, 2000), which in turn influences departure dates (Saino et al., 2004; Studds and Marra, 2005), condition during migration (Bearhop et al., 2004) and migration speed (Tøttrup et al., 2008), all of which influence both survival and the timing of arrival on the breeding grounds. Earlier arrival increases breeding success due to the advantages of early arrival for territory selection, mate choice, the number of breeding attempts and fledgling survival, amongst others (Aebischer et al., 1996; Kokko, 1999; Møller, 1994; Norris et al., 2004; Potti, 1998; Saino et al., 2004; Smith and Moore, 2005). Consequently, wintering habitat has carry-over effects for many aspects of life history, especially breeding success and fitness (Marra et al., 1998; Marra and Holmes, 2001; Norris, 2005; Studds and Marra, 2005; Webster et al., 2002), and so can greatly influence population dynamics.

The scale at which a migrant is a habitat generalist or specialist during winter determines many aspects of wintering ecology and winter habitat selection, both of which have implications for population dynamics. Upon arrival at the wintering grounds there is a trade-off between locating optimal habitat and reducing the costs of migration. Wintering in poor habitat can reduce both short and long-term survival and fitness (Duriez et al., 2012; Norris, 2005; Norris et al., 2004), yet the costs of migration increase with the time taken to establish a territory because the risk of mortality is high during migration (Newton, 2010a, 2006b). If conditions change during winter, moving to new areas can further reduce survival because predation

risk is also higher when surroundings are unfamiliar and the ability to find food is compromised, and so the benefits of residency are lost (Cresswell, 2014; Cuadrado, 1997; Hedenström, 2008; Lind and Cresswell, 2006; Piper, 2011; Yoder et al., 2004). The ability to utilise a wide range of habitat features – i.e. generalist winter habitat requirements within a wintering habitat – therefore maximises survival and future fitness by lessening the implications of wintering in sub-optimal habitat, increasing potential habitat availability, and providing resilience to habitat loss or change both within and between winters by removing the need to relocate. Because initial site selection within the wintering range by juveniles during their first migration is most likely stochastic at the large scale and conditions on the wintering grounds are chiefly unknown (the serial residency hypothesis; Cresswell, 2014), migrants are predicted to have non-specialist winter habitat requirements (Cresswell, 2014). If the scope of potential wintering habitat and suitable wintering conditions are increased, the ability to locate a wintering territory upon arrival and remain in that territory is increased, especially for naïve juveniles arriving in unknown areas. This is one likely explanation for why many migrants are found to winter in sub-optimal habitats (Askins et al., 1990; Rappole et al., 1983; Rappole et al., 1989).

Nevertheless, densities of migrant species often vary in different habitats throughout their wintering range (e.g. Sherry and Holmes, 1996), and so it is likely that habitat selection does occur on some scale. Furthermore, because of the influence of winter habitat on survival and future breeding success, some species exhibit dominance-based habitat occupancy on the wintering grounds, in which individuals complete for territories of higher quality. As a consequence, some individuals inevitably must then winter in less optimal habitats (Jones et al., 1996b; Marra and Holmes, 2001; Rappole et al., 1989; Robbins et al., 1989). Because of the resulting relationship between winter territory habitat characteristics, body condition and demographics (Catry et al., 2004a; Figuerola et al., 2001; Lynch et al., 1985; Marra and Holmes, 2001; Parrish and Sherry, 1994), the survival and reproductive success of these individuals may be reduced as a result (Marra and Holmes, 2001; Norris et al., 2004; Reudink et al., 2009). Where to establish a winter territory and whether to compete with conspecifics for territories where habitat

quality differs may still be an important decision for some wintering migrant species. Even if individuals do not select territories based on territory quality (i.e. there is a lack of dominance or arrival-based territory occupancy), it is probable that individuals respond to heterogeneity in habitat characteristics and territory quality in other ways, such as by adjusting territory size (Carpenter et al., 1983; Smith and Shugart, 1987) or with non-random space use within territories (Barg et al., 2006).

Despite the importance of winter habitat for population dynamics, even basic knowledge of wintering ecology and habitat use is lacking for the majority of migrant species (Sanderson et al., 2006; Sillett and Holmes, 2002; Vickery et al., 2014). Many of these species have shown dramatic declines in recent decades, especially long-distance migrants (Sanderson et al., 2006; Thaxter et al., 2010; Vickery et al., 2014). Winter habitat degradation has been suggested as a main driver of declines in almost one third of Nearctic migrants (Rappole and McDonald, 1994), and for several Palearctic migrants (Baillie and Peach, 1992; Vickery et al., 2014); yet some studies suggest that wintering conditions may be less limiting than previously thought (Hulme and Cresswell, 2012; Wilson and Cresswell, 2006). Knowledge of wintering ecology and degree of habitat specialism is therefore essential to conservation efforts in both the wintering and breeding grounds (Sherry and Holmes, 1996). The scale at which migrants are habitat generalists, the scale of variation in habitat quality across individuals, and how individuals respond to the suite of habitat characteristics within their territories and any changes throughout winter can give insights into population resilience to anthropogenic habitat loss.

Here we establish to what degree and at what scale a long-distance Palearctic migrant, the whinchat, is a winter habitat generalist within its wintering habitat of open savannah, and the influence of age and sex on winter territory selection. Whinchats are found in a wide range of natural and human-modified habitats on their wintering grounds in West Africa (Hulme and Cresswell, 2012). Populations have declined dramatically across the breeding range (Vickery et al., 2014). Although there is strong evidence for summer conditions to be a major cause of the declines

(Britschgi et al., 2006; Müller et al., 2005), we lack the knowledge of wintering ecology necessary to determine the role of wintering conditions in these declines.

As a long-distance passerine migrant, we predict that whinchats will have non-specialist winter habitat requirements at the territory-scale: that habitat characteristics vary widely across territories, and that territories will be maintained even if habitat changes substantially throughout winter. We predict to find no evidence of dominance-based habitat selection: that territory habitat characteristics do not differ according to the age and sex of an individual, and instead that any response to heterogeneity in habitat characteristics is an adjustment of territory size and a preference for using key but general habitat features within territories.

We therefore test whether:

1. Whinchats are habitat generalists or habitat specialists, by describing the range of habitat characteristics across territories and the degree to which habitat characteristics change within territories throughout winter.

2. Whether whinchats show dominance-based territory occupancy, by testing whether habitat characteristics within territories are related to the age, sex and body condition of occupants.

3. How individuals respond to habitat heterogeneity at the territory-level, by testing whether territory habitat characteristics influence territory size, and whether specific habitat features influence space use within territories. Because perches are an important feature for whinchats (Fischer et al., 2012; Hulme and Cresswell, 2012), relationships between habitat characteristics and territory use may differ in farmland with structural crops if these crops substitute for perches. We therefore also test the interaction between shrub score and maize when exploring the influence of habitat characteristics on space use within territories.

4.3 Methods

Habitat sampling

For details of study sites, resighting protocol, and calculating territory size, see Chapter 2: *General methodology*.

Territory habitat characteristics were sampled for 84 birds: 34 ringed in winter 1 (of which 21 were resighted in winter 2 also) and 50 ringed in winter 2. Habitat was surveyed in winter 2 between the end of January and April, with the majority of habitat sampling carried out before mid-March. All individuals had been resighted at least five times to determine the territory centre and areas of use within the territory (see Chapter 2: *General methodology*). For the 21 birds resighted in both winters 1 and 2, we used sightings from winter 2 to locate sampling plots. 13 birds that were ringed in winter 1 were not resighted in winter 2, so in this case, because all individuals return to the same winter territories (see Chapter 3: *Site fidelity*), we used resighting locations from winter 1 to locate habitat plots and compared photographs of the territory in both years to ensure that the habitat features recorded had not changed substantially. In all cases, territory habitat characteristics had not changed substantially between years and habitat surveys were undertaken.

Habitat variables recorded are listed in Table 4.1. Three circular plots were sampled within each territory: one 50 m diameter plot (~1950 m^2) at the centre of the territory, determined from average longitude and latitude coordinates for all resightings, and two 10 m diameter plots (~80 m^2 each) within the territory (1) where the bird was seen most often ('present' plot) and (2) in an area that the bird was never seen ('absent' plot). Locations for 'present' and 'absent' plots were found by visually examining resightings in ArcMAP 10.1 (ERSI, 2012). For the 'present' plot, we located coordinates closest to all resightings (ensuring that the plot would include at least one resighting location), and for the 'absent' plot we used the ruler tool to find coordinates within the territory that were the furthest distance from all resightings. We surveyed both 10 m plots for 73 birds, and only 'absent' plots for

seven additional birds because poor weather curtailed the survey period. To explore changes in territory habitat characteristics over the winter, 30 m diameter plots (~705 m^2) were surveyed 1) at the beginning (October) and 2) at the end (late February) of winter 3 for 14 individuals that returned to the territory used in winter 2. We chose 30 m because this was the largest plot that realistically allowed habitat variables to be surveyed at a fine detail. Because territory locations were the same in both years (see Chapter 3: *Site fidelity*), 30 m plots were surveyed where 50 m plots had been surveyed in the previous winter (i.e. the territory centre), the locations of which were marked to allow accurate relocation later in the year. For all plots, we calculated further variables from the raw data (details in Tables 4.1 and 4.2).

Table 4.1. Description of habitat variables measured during habitat surveys and the plot(s) for which the variable was measured: A = 50 m, B = 30 m (start/end), C = 10 m (present/absent), plus variables calculated for inclusion in PCA analyses.

Variable	Description
Plant, shrub and tree count (A,C)	Each identified to species level and counted in size categories: 1) 30-60 cm; 2) 60-200 cm; 3) 2-4 m; 4) 4-8 m; 5) >8 m. Plants of the same species sharing >50% of their canopy were counted as one plant.
Shrub leaf cover (C)	Leaf cover of each shrub scored on a scale of 0-4, representing 25% cover categories (4 = 100% cover)
Land type (A,B,C)	% cover of: pasture, old farm (>2 years old), farmland
Herb cover (A)	% cover of herbaceous vegetation (including shrubs <30 cm): 0-25% / 26-50% / 51-75% / 76-100%
Ground cover (B,C)	% cover of: bare ground, litter and short grass, long grass, herbaceous vegetation, shrubs
Grazing (A,B,C)	Level of grazing pressure: none / low / high)
Human activity (A,B,C)	Evidence of people using the immediate area: none / low / high
Plant diversity*	Shannon-Wiener index of plant species diversity
Green plant score*	The number of plants in each height category multiplied by the height category
Perching shrub score*	The number of perching shrubs in each height category multiplied by the size category (1-5)
Shrub score*	The score of green plants x 1 and score of perching shrubs x 2
Vegetation score*	The number of plants in each category multiplied by the size category (1-5), summed
Total plants*	Total of tree and shrub count across all species

* variables calculated from plant, shrub and tree counts

Larger habitat characteristics, such as the area of large patches of shrubs and trees, could not be measured effectively at ground level. We therefore used satellite photographs of territories to survey these features. Images were obtained from Google Earth (Google, 2012) between 1st and 31st May 2013 and had been taken within three months of habitat sampling. Photographs of territories, field notes, and comparison of satellite images taken over three months before and after the period of habitat sampling confirmed that larger features remained unchanged at the scale at which we were measuring. To measure vegetation cover at a large scale, a circular grid equal to 1 x 1 m was digitally placed over images covering the same area as the 50 m plot surveyed, and each patch of vegetation covering > 50% of one 1 x 1 m square was counted. Each patch was scored for the number of contiguous squares it covered and the minimum distance (in metres) to the next nearest vegetation patch that also covered > 50% of any 1 x 1 m square. From these data, the number of patches, the average patch size (m^2), the average distance between patches (m), and the cover of dense vegetation (proportion of all squares covered in %) were obtained.

Statistical analyses

Principle component analyses

For both 50 m and 10 m sample plots, we conducted principle components analyses (PCA) to reduce the number of habitat variables and to account for correlated variables (Table 4.2). In both cases, an orthogonal Varimax rotation (Kaiser, 1958) was applied to aide interpretation. We chose a suite of habitat variables based on whether their inclusion produced interpretable PCA results: excluded variables were modelled separately in later analyses providing that no collinearity resulted. Extracted axes ('components') were retained if their Eigenvalue was at least one (i.e. the component contributed to at least 10% of the total variation) (Abdi and Williams, 2010). A variable was considered to contribute to a component if the loading was at least ±0.4 after rotation. For habitat variables within 50 m plots, the analysis yielded three axes with eigenvalues >1 accounting for 86% of the total variation from 10

original variables (Table 4.2). High scores for the first principle component (PC1, 58% of the total variation) implied a lower number of shrubs, particularly perching shrubs, and fewer individual plants: PC1 was therefore named 'shrub score'. Note that the scores were later inverted for all further analyses so that a higher score related to higher shrub density. High scores for the second component (PC2, 18% of the total variation) implied that any patches of vegetation were small and the total amount of vegetation in the territory was low: PC2 was therefore named 'vegetation cover'. High scores for the third component (PC3, 10% of the total variation) implied that number of green plants was low and that patches of vegetation were sparse and far apart: PC3 was therefore named 'vegetation clumping'. For the 10 m plots, the analyses also yielded three axes with eigenvalues >1 accounting for 83% of the total variation from eight original variables (Table 4.2). Similar to 50 m results, high scores for the first component (PC1, 51% of the total variation) implied a lower number of perching shrubs and fewer individual plants: PC1 was therefore also named 'shrub score', and was also later inverted so that a higher score related to higher shrub density. High scores for the second component (PC2, 18% of the total variation) implied low litter cover and high grass cover: PC2 was therefore named 'amount of grass'. High scores for the third component (PC3, 13% of the total variation) implied high plant diversity and a large number of green plants: PC3 was therefore named 'plant diversity score'.

Sample sizes

Birds which could not be confidently aged or sexed were excluded from models including age and sex as predictors. One individual was excluded from all analyses as its territory was in an unrepresentative habitat (dense coffee farm), which grossly inflated any vegetation counts within that territory. Nonetheless, removing this individual did not change the main findings from any analyses.

Table 4.2. Results of the three top 'components' (i.e. variables) derived from principle component analyses on a range of habitat variables for both 50 m (*n* = 83) and 10 m (*n* = 159) sample plots, plus the variables contributing to each component (those with loadings of at least ±0.4 following a Varimax rotation). For 50 m plots, six further extracted axes (not shown) cumulatively explained less than 15% of the total variation in habitat variables. For 10 m plots, five further extracted axes (not shown) cumulatively explained less than 17% of the total variation in habitat variables. Habitat variables only included in analyses for one plot type are shown in italics.

	Principle component					
	50 m			10 m		
	1 Shrub score	2 Vegetation cover	3 Vegetation clumping	1 Shrub score	2 Amount of grass	3 Plant diversity score
Standard deviation	2.28	1.26	0.85	2.03	1.22	1.02
Explained variance	58%	18%	10%	51%	18%	13%
Cumulative variance	58%	75%	86%	51%	70%	83%
	Variable loadings following Varimax Rotation					
	50 m plots			10 m plots (present/absent)		
Total shrub score	-0.51			-0.52		
Perching shrub score	-0.54			-0.59		
Total plants	-0.46			-0.44		
% Shrub cover				-0.42		
Vegetation score	-0.47					
Average patch size		-0.70				
% Vegetation cover		-0.59				
Number of patches			-0.56			
Average distance between patches			0.54			
Green plant score			-0.49			0.64
Plant diversity						0.69
% Litter cover					-0.70	
% Grass cover					0.69	

Analyses were performed in R version 3.0.1 (R Development Core Team, 2013) and RStudio Version 0.98.507. Data were checked for normality when necessary and for multicollinearity using variance inflation factors (CARS package; Fox and Weisberg, 2010). The Shannon-Wiener Species Diversity Index was calculated from the number of total number and proportion of each plant species recorded in each plot, subsequently referred to as 'plant diversity', where a higher number indicates higher species diversity (Shannon, 2001). Paired *t*-tests and paired Wilcoxon tests were used to assess changes in habitat characteristics over the winter. Standard *t*-tests and Wilcoxon tests were used to explore differences in habitat characteristics between territories of males and females, and first-winter and adult birds. The sequential Bonferroni procedure (Rice, 1989) was used to correct for Type 1 error rate. Predictors of territory size were explored with General Linear Models, and predictors of space use within territories were explored with Generalised Liner Models (logistic regression).

Multiple regression model simplification was based on Akaike Information Criterion (AIC) (Bozdogan, 1987), where variables failing to improve AIC or add a significant contribution to the model (as determined by a non-significant ANOVA performed between models) were removed from the model. For models where all variables had the same or similar sample sizes, dredge analyses were used to identify minimal models (Bartoń, 2012): cases with missing values were removed from the dataset as required for dredge analyses, and resulting minimal adequate models were produced using complete datasets. We chose ΔAICc = 3 as a threshold for which models to present from dredge analyses because this value contained what we felt were a representative number of models (ΔAICc = 2 too few and ΔAICc = 4 too many). Model fits were evaluated from diagnostic model plots and models presented if assumptions were reasonably met (Crawley, 2007). Mean values are presented as means ± one standard error in all cases. Test-specific samples sizes are presented as accordingly within tables and results. A statistical significance level of $p < 0.05$ was chosen to reject null hypotheses.

4.4 Results

1. Variation in habitat characteristics

Habitat characteristics varied substantially across individual territories (Table 4.3, Figure 4.1; *n* = 83). Most territories were situated in pasture (72 of 83 territories), with territories also situated amongst active crop fields (*n* = 8) and on old farmland (*n* = 3). The average whinchat territory had low levels of grazing, low levels of human disturbance and some chopping. The average territory sample plot contained active farmland (11%). When maize was present within a territory sample plot, maize made up n average 57% (± 11.9%) of the territory plot (*n* = 10/82 territories).

Table 4.3. The range of habitat characteristics observed within habitat plots across all territories (*n* = 83) as either mean values (± SE), or number of territories. Where a characteristic was present, the number of territories where this characteristic occurred in high or low values is also presented (see *methods* and Table 4.1 for detailed descriptions of how habitat characteristics were categorised).

Habitat characteristic	*Average* (± SE)	*Range*
% Farmland	11.3% (±2.9)	0 – 100%
% Maize	6.9% (±2.5)	0 – 100%
% Other crop type	4.4% (±1.8)	0 – 100%
Plant diversity	1.37 (±0.05)	0 – 2.39
	Number of territories (*n* = 82)	
	Absent	*Present (low/high)*
Maize	72	10
Human disturbance	2	80 (52/30)
Degree of chopping	29	52 (48/6)
Level of grazing	2	80 (44/47)

Habitat characteristics changed significantly between the start and the end of the winter (Table 4.4, Figure 4.2). Specifically, the amount of long grass decreased, the amount of bare ground increased, and shrubs had sparser leaf coverage at the end of the winter. Grazing intensity increased as the winter progressed.

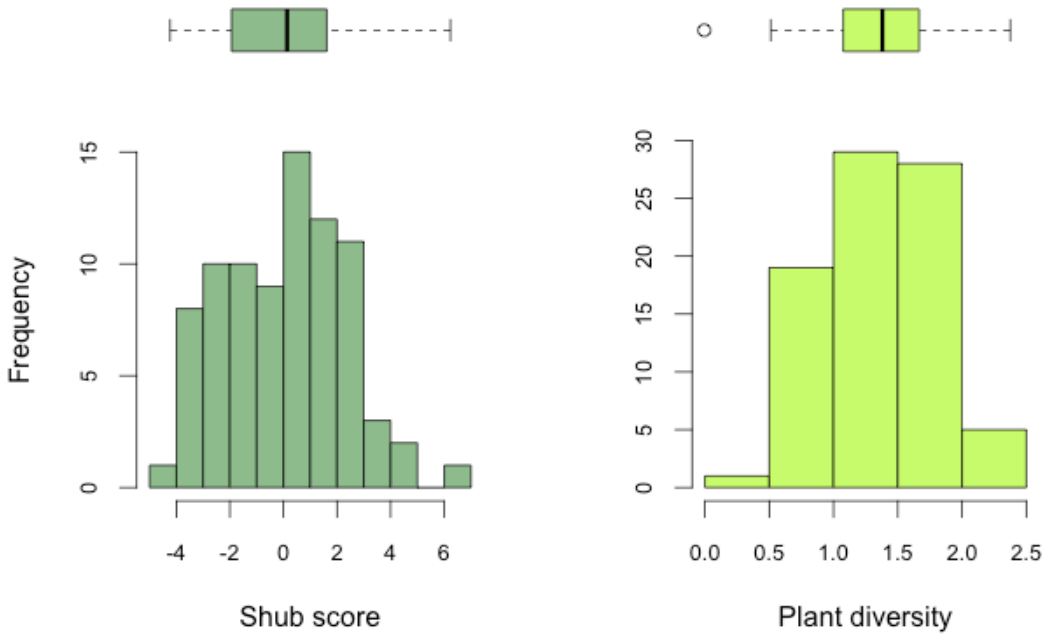


Figure 4.1. The variation and range in shrub density (shrub score) and plant diversity (Shannon index) across all territories (*n* = 82; one case excluded due to missing data), where -4 indicates the lowest and 6 indicates the highest shrub density, and 2.5 indicates the highest plant diversity).

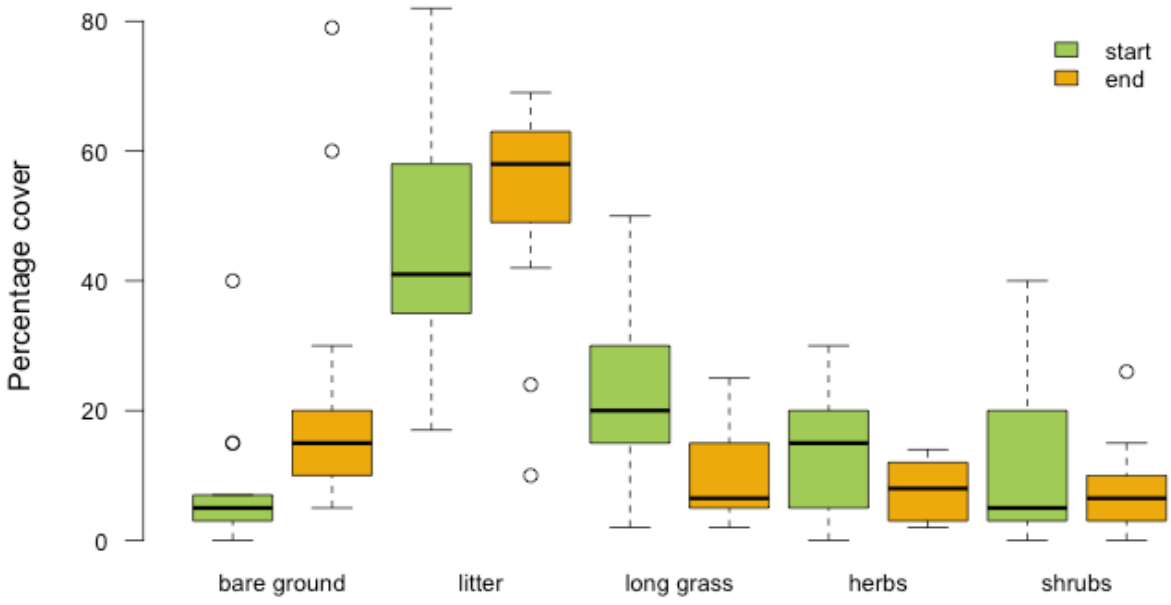


Figure 4.2. Change in habitat characteristics within territories from the start (green) to the end (orange) of the winter. The amount of bare ground, long grass and amount of herbs changed significantly, whereas the amount of leaf litter and shrubs remained unchanged (see Table 4.4 for sample sizes, means and statistical tests).

Table 4.4. Results of paired *t*-tests (#) and paired Wilcoxon tests (*) to assess changes in habitat characteristics within territories between the start and the end of the winter. Sample size for average leaf cover is lower due to the absence of shrubs in some plots. Significant *p* values are shown in bold

Habitat characteristic	*n*	*t* / V	df	*p*	*Bonferroni* adjusted *p*	Mean (start)	Mean (end)
% Bare ground *	14	5.5		**0.0035**	**0.0045**	8 (±2.5)	22 (±5.3)
% Long grass #	14	3.9	13	**0.0017**	**0.0042**	25 (±3.8)	10 (±1.9)
% Litter #	14	-1.2	13	0.15		41 (±5.3)	53 (±4.3)
% Herbs #	14	3.4	13	**0.0051**	**0.0056**	15 (±2.4)	8 (±1.1)
% Shrub *	13	25		0.075		10 (±2.7)	7 (±1.7)
Shrub leaf score:							
No leaves *	14	0		**0.0059**	**0.0063**	0.06 (±0.063)	8.8 (±3.0)
Leaf cover = 1-24% *	14	13.5		0.17		3.0 (±1.3)	7.2 (±2.3)
Leaf cover = 25-49% *	14	65		**0.045**		10.3 (±4.4)	1.9 (±0.52)
Leaf cover = 50-74% *	14	66		**0.0038**	**0.0050**	8.3 (±2.9)	1.2 (±0.73)
Leaf cover = 75-100% *	14	0		**0.034**		0.44 (±0.30)	1.7 (±0.66)
Average shrub leaf score	12	2.7	11	**0.021**		2 (±0.10)	1.4 (±0.29)
Amount of grazing *	13	0		**0.0060**			

2. Evidence for dominance-based territory occupancy

There were no significant differences in shrub score, vegetation cover or clumping, plant diversity, percentage of farmland or maize, grazing intensity or the amount of herbaceous vegetation between the territories of males and females, or first-winter and adult birds (Table 4.5, Figure 4.3).

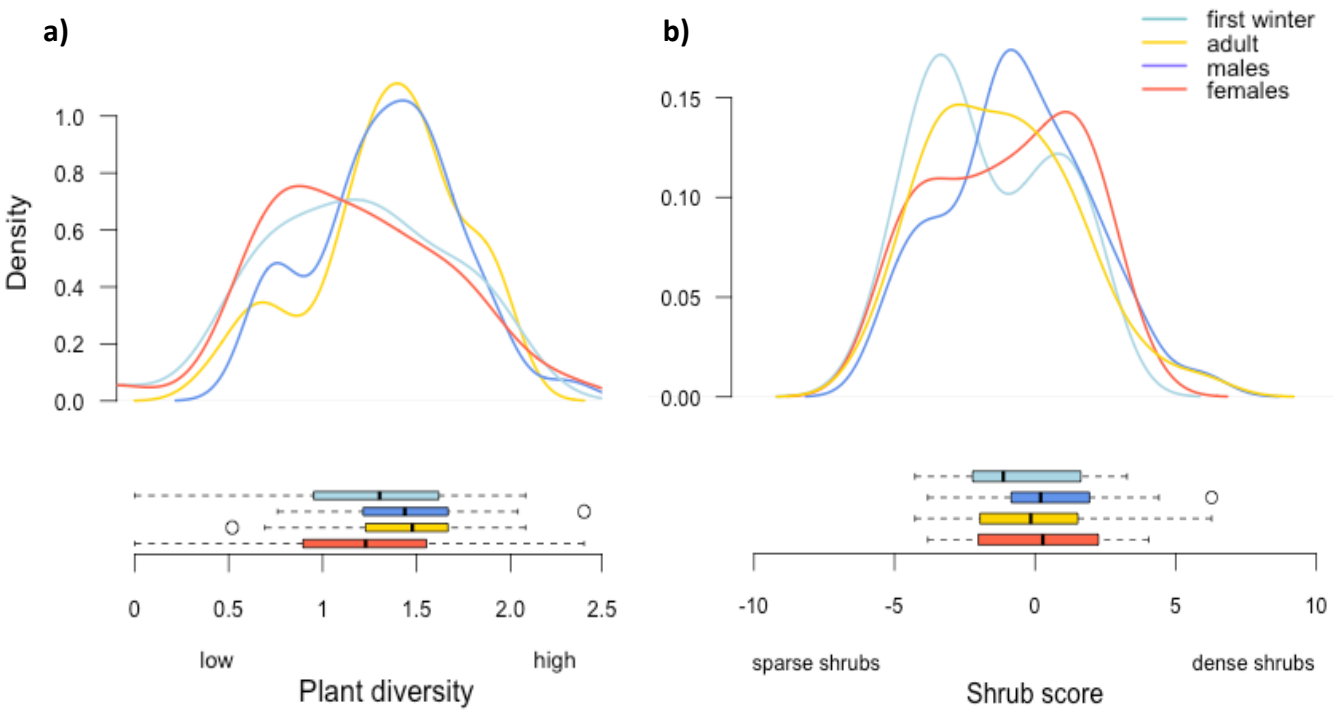


Figure 4.3. The range of **a)** plant diversity and **b)** shrub density ('shrub score') amongst all territories, split by age and sex. Colours lines (top charts) show kernel density; box plots (bottom charts) show the range between first-winter and adults, and males and females. Sample sizes vary because age and sex was unknown for some individuals.

3. Predictors of territory size and space use within territories

Average territory diameter across winters 1 and 2 was 65 m (±1.9 m), range 76 m, *n* = 83). Individuals had smaller territories if shrubs were at a higher density and maize was present within the territory (Figure 4.4; Tables 4.6 and 4.7). None of the other territory habitat characteristics explored influenced territory size (Tables 4.6 and 4.7).

Within winters, whinchats used areas of their territories that had significantly more perching shrubs (Figure 4.5; Tables 4.8 and 4.9). No other habitat characteristics influenced space use within territories.

Table 4.5. The range of habitat characteristics observed within habitat plots across all territories according to age and sex (*n* = 83, although sample sizes vary because age and sex was unknown for some individuals) plus results of *t*-tests (#) and Wilcoxon tests (*) to assess differences between territories of males (♂) and females (♀), and first-winter and adult birds. Degrees of freedom are given for *t*-tests and sample sizes for Wilcoxon tests. Note that shrub cover, vegetation cover and vegetation clumping are variables derived from principle component analyses (see *methods* and Figures 4.1 & 4.3 for the scale and variation of these variables).

	Average (± SE)			
Habitat characteristic	♂	♀	1st winter	Adult
Shrub score	-0.079 (±0.37)	0.096 (±0.41)	-0.52 (±0.35)	0.25 (±0.40)
Vegetation cover	0.072 (±0.14)	0.034 (±0.23)	-0.083 (±0.22)	-0.0072 (±0.19)
Vegetation clumping	0.077 (±0.15)	-0.051 (±0.17)	-0.047 (±0.13)	0.0090 (±0.18)
Plant diversity (*Shannon index)*	1.43 (±0.062)	1.26 (±0.087)	1.27 (±0.078)	1.44 (±0.062)
% Farmland *if present*	50.0% (±13.5)	56.3% (±11.2)	55.0% (±10.6)	53.0% (±12.3)
…of which: % maize	55.0% (±21.9)	59.2% (±14.4)	57.9% (±15.3)	53.3% (±21.3)
% other crop	45.0% (±18.9)	35.0% (±16.1)	42.5% (±14.8)	52.5% (±12.5)

	♂ vs. ♀			1st winter vs. Adult		
	t / W	df / *n*	*p*	*t* / W	df / *n*	*p*
Shrub score #*	-0.3	72	0.75	590	*75*	0.23
Vegetation cover **	621	*74*	0.55	756	*75*	0.58
Vegetation clumping ##	0.6	72	0.58	-0.3	65.2	0.80
Plant diversity *#	1.7	*74*	0.10	-1.7	*73*	0.087
% Farmland (all territories) **	640	*74*	0.59	828	*75*	0.072
% Maize (all territories) **	619	*74*	0.30	774	*75*	0.21
Amount of herbs **	772.5	*74*	0.21	771.5	*75*	0.38
Level of grazing **	761	*74*	0.30	656	*75*	0.57

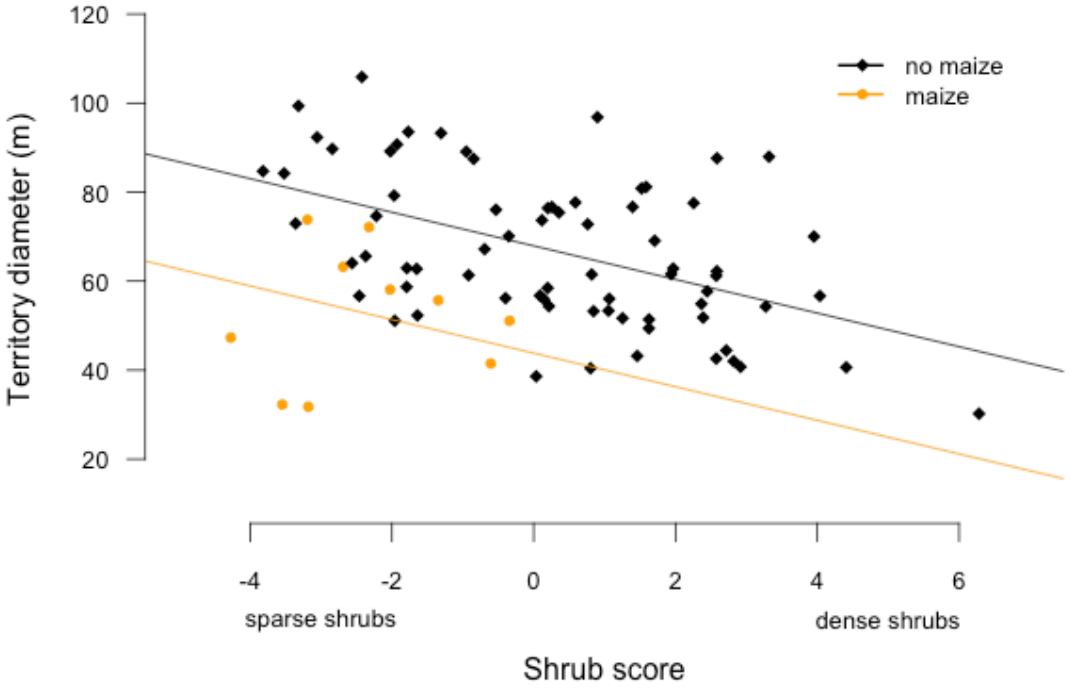


Figure 4.4. Territory size as a response of the amount of perching shrubs in the territory ('shrub score'), either if maize was present (•) or absent (•) in the territory, where a more positive shrub score represents more shrubs in the territory (*n* = 82; one case excluded due to missing data). Lines show predicted values of territory size index from the model presented in Tables 4.6 and 4.7, both if maize was present (–) or absent (–) from the territory and shrub score average. Birds had larger territories if there were fewer shrubs and maize was present within their territory.

Table 4.6. The top 16 models (within 3 AICc of the top model*) of all possible General Linear Models exploring predictors of territory size in whinchats during winter, from the initial maximal model of: territory size ~ age + sex + bird size + shrub score + vegetation cover + vegetation clumping + presence of maize + % non-maize crops + main land type + plant diversity. The interaction between age and sex was not significant; *n* = 78 (five cases excluded from dredge analysis due to missing data)

Component	Log Likelihood	AICc	ΔAICc	Weight
Shrub score + maize	-319.5	647.5	0.00	0.14
Shrub score + maize + main land type	-317.2	647.6	0.08	0.13
Shrub score + maize + % other crops	-318.8	648.4	0.93	0.09
Shrub score + maize + vegetation cover	-318.9	648.6	1.09	0.08
Shrub score + maize + main land type + body size	-316.5	648.6	1.14	0.08
Shrub score + maize + body size	-319.1	649.0	1.05	0.07
Shrub score + maize + main land type + vegetation cover	-316.9	649.5	2.00	0.05
Shrub score + maize + plant diversity	-319.3	649.5	2.01	0.05
Shrub score + maize + main land type + plant diversity	-317.0	649.6	2.13	0.05
Shrub score + maize + main land type + vegetation clumping	-317.1	649.7	2.23	0.05
Shrub score + maize + vegetation clumping	-319.5	649.7	2.25	0.04
Shrub score + maize + body size + % other crops	-318.4	649.9	2.40	0.04
Shrub score + maize + main land type + % other crops	-317.1	649.9	2.40	0.04
Shrub score + maize + % other crops + vegetation cover	-318.5	650.2	2.75	0.03
Shrub score + maize + body size + vegetation cover	-318.6	650.3	2.84	0.03
Shrub score + maize + % other crops + plant diversity	-318.6	650.4	2.93	0.03

* 3 AIC chosen to give a representative number of top models

Table 4.7. Results from General Linear Models exploring predictors of territory size of whinchats during winter. The first model (the initial maximal model of: territory size ~ age + sex + bird size + shrub score + vegetation cover + vegetation clumping + presence of maize + % non-maize crops + main land type + plant diversity) is presented as the results from a dredge analysis averaging the top 16 models (within 3 AICc of the top model*), along with the minimal top model. Residual SE for top model = 7.48 on 79 df; adjusted R-squared = 0.26; $F_{2,79}$ = 15.2; overall *p*-value = <0.0001. The interaction between age and sex was not significant. Note that the reference category for main land type is pasture; *n* = 78 and 82 for dredge analysis and minimal model, respectively (five and one cases excluded from full and minimal model respectively due to missing data).

	Full model		All models delta AIC < 3			Top model			
Variable	*z*	*p*	Model-averaged parameter estimate	SE	Relative weight	Parameter estimate	SE	*t*	*p*
(Intercept)	23.0	**<0.0001**	68.44	2.94		67.90	1.78	38.1	**<0.0001**
Shrub score	4.2	**<0.0001**	-3.63	0.85	1.00	-3.78	0.79	-4.8	**<0.0001**
Maize (present)	3.9	**<0.001**	-24.28	6.17	1.00	-24.09	5.48	-4.4	**<0.0001**
Land type: crop	1.4	0.16	10.59	7.40	0.39				
Land type: old farm	1.2	0.23	-10.91	8.91					
% Other crops	0.9	0.39	0.10	0.12	0.24				
Vegetation cover	0.9	0.39	-1.23	1.41	0.20				
Body size	1.0	0.35	2.01	2.19	0.22				
Plant diversity	0.5	0.59	-2.26	4.12	0.13				
Vegetation clumping	0.3	0.74	0.63	1.86	0.09				

* 3 AIC chosen to give a representative number of top models

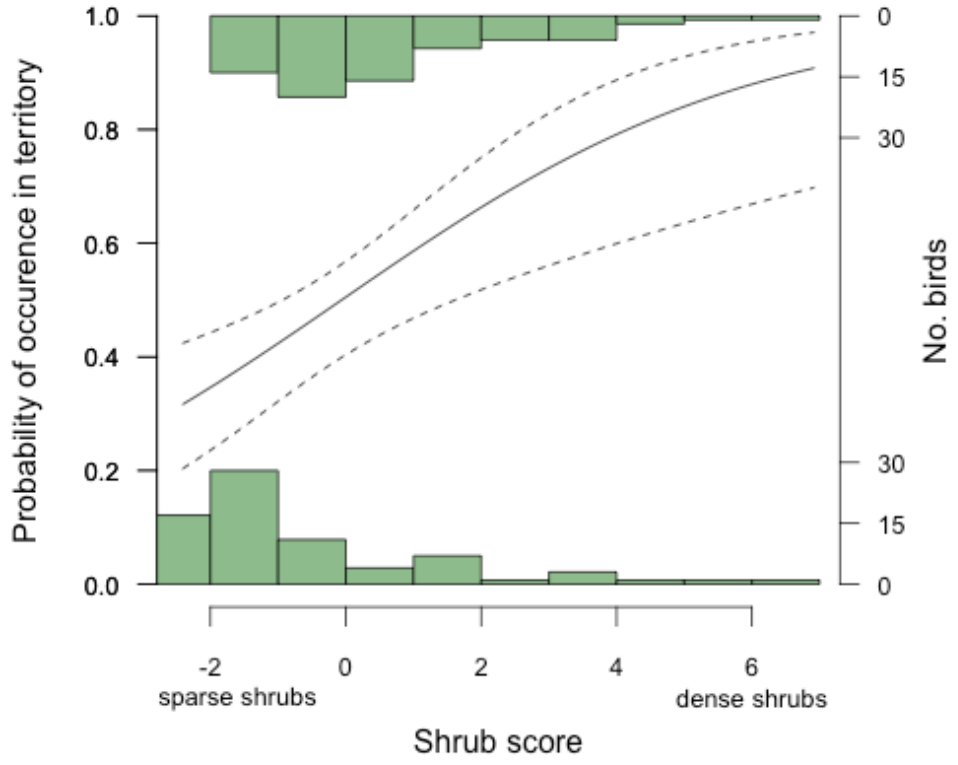


Figure 4.5. The probability of sighting a bird within an area of its territory ('present' plot) or not seeing a bird within an area of its territory ('absent' plot) in relation to the amount of perching shrubs within that area. Lines show values (solid line) with confidence intervals (dashed lines) as predicted from the model presented in Tables 4.8 and 4.9; histograms show the distribution of shrub score amongst present and absent plots. Total number of complete pairs = 74 (*n* = 148; note that for seven of 80 birds, only 'absent' plots were recorded).

Table 4.8. The top 16 models (all models within 3 AICc of the top model*) of all possible logistic regression models exploring predictors of presence or absence (i.e. favoured areas) *within* territories, from the initial maximal model of: presence ~ winter (study year) + presence of maize + amount of herbs + main land type + human disturbance + level of grazing + shrub score + amount of grass + plant diversity score + shrub score*presence of maize, controlling for individual territory. For final model, *n* = 148, number of observations = 74 complete pairs (note that for seven of 80 individuals, only absent plots were surveyed).

Component	Log Likelihood	AICc	ΔAICc	Weight
Shrub score	-99.69	205.5	0.00	0.17
Shrub score + level of grazing	-99.31	206.9	1.34	0.09
Shrub score + amount of herbs	-99.33	206.9	1.38	0.09
Shrub score + disturbance	-99.40	207.1	1.52	0.08
Shrub score + main land type	-99.47	207.2	1.65	0.07
Shrub score + amount of grass	-99.49	207.2	1.71	0.07
Shrub score + plant diversity score	-99.55	207.4	1.83	0.07
Shrub score + winter	-99.68	207.6	2.09	0.06
Shrub score + presence of maize	-99.69	207.7	2.10	0.06
Shrub score + presence of maize + shrub * maize	-98.89	208.2	2.64	0.05
Shrub score + level of grazing + amount of herbs	-98.93	208.3	2.72	0.04
Shrub score + amount of herbs + disturbance	-99.01	208.4	2.88	0.04
Shrub score + level of grazing + plant diversity score	-99.01	208.4	2.89	0.04
Shrub score + amount of herbs + disturbance	-99.02	208.4	2.90	0.04
Shrub score + level of grazing + amount of grass	-99.07	208.5	3.00	0.04

* 3 AIC chosen to give a representative number of top models

Table 4.9. Results from logistic regression analyses exploring predictors of presence or absence (i.e. favoured areas) *within* territories. The first model (initial maximal model of: presence ~ winter (study year) + presence of maize + % herbs + main land type + human disturbance + amount of grazing + shrub score + amount of grass + plant diversity score + shrub score*presence of maize, controlling for individual territory) is presented as is the results from a dredge analysis averaging the top 16 models (all models within 3 AICc of the top model*), along with the minimal top model. Significant values are shown in bold. Deviance for top model = 207.78 on 157 df; AIC = 213.8. Note that main land type = pasture and winter 1 are the reference categories, and that the density of perching shrubs increases as shrub score increases. For final model, number of complete pairs = 74 (note that for seven of 80 individuals, only absent plots were surveyed).

	Full model		All models ΔAICc < 3			Top model			
Variable	*z*	*p*	Model-averaged parameter estimate	SE	Relative weight	Parameter estimate	SE	*z*	*p*
(Intercept)	0.4	0.66	-0.170	0.39		-0.079	0.17	-0.5	0.63
Shrub score	3.4	**<0.001**	0.326	0.095	1.00	0.29	0.09	-3.3	**0.0010**
Grazing	0.9	0.36	0.274	0.30	0.25				
Herbs	0.8	0.40	-0.024	0.03	0.17				
Disturbance	0.8	0.44	0.251	0.33	0.16				
Main land type (crop)	0.7	0.51	-0.392	0.59	0.07				
Amount of grass	0.7	0.51	0.091	0.14	0.11				
Plant diversity score	0.6	0.54	0.113	0.18	0.11				
Winter (2)	0.2	0.88	0.069	0.46	0.06				
Maize (present)	0.3	0.73	-0.401	1.15	0.10				
Maize (present) * shrub score	1.0	0.32	-0.827	0.82	0.05				

* 3 AIC chosen to give a representative number of top models

4.5 Discussion

Evidence for generalist winter habitat requirements

Our findings of possibly large variation (discussed below) in territory habitat characteristics across territories, variation in the land-types in which territories had been established, and significant temporal changes in habitat characteristics within territories of resident birds all suggest that whinchats are non-specialists during the winter.

We believe that our results show large variation in habitat characteristics across individual territories. For example, the percentage of farmland within territory plots ranged from 0 – 100%, with maximum variation of 0 – 100% for both cover of maize and other crop types; plant diversity index varied from 0 to 2.39, equivalent to 1 – 17 plant species within territory plots; and the level of both grazing and human disturbance ranged across all recorded levels, with quite similar numbers of territories with either high or low intensities. As seen in Figures 4.1 and 4.3, the range of both shrub score and plant diversity recorded was also spread quite widely across territories. In short, territories probably varied from fairly typical open Guinea savannah through to completely anthropogenic-modified monoculture.

The ability to utilise a wide range of habitats would allow naïve individuals arriving in unknown areas, such as juvenile birds undertaking their first migration, to establish, maintain and survive in winter territories in sub-optimal habitats, thereby reducing migration time and the costs of moving. The ability to overwinter in a range of habitats without implications for survival (see Chapter 5: *Survival* for a discussion of this) also increases the availability of suitable habitat, especially when wintering conditions are unpredictable and vary between years, as they often do in Africa (e.g. Gordo et al., 2005). By adapting to changes within their territories, whinchats avoid having to relocate during the winter and so benefit from being resident. Whinchats were observed to use several foraging strategies, such as foraging on the ground, gleaning from vegetation, and fly catching, and so may adapt to changes by adjusting

their foraging strategy, thus allowing them to obtain enough food resources in a variety of habitats. Pied flycatchers *Ficedula hypoleuca* are able to hold winter territories because of their diverse foraging strategy, for example, whereas willow warblers *Phylloscopus trochilus* are forced to be itinerant due to more specialist requirements (Salewski et al., 2002a). Fewer abiotic constraints and more predictable foraging opportunities on the wintering grounds also mean that optimal body mass is likely to be lower during winter, requiring fewer resources and allowing birds to overwinter in relatively poor habitats without compromising survival (see Lima, 1986 for a review of the starvation-predation risk trade-off). Non-specialist habitat requirements most likely also allow whinchats to maintain their wintering strategy of extremely high winter site fidelity if habitat changes between winters (see Chapter 3: *Site fidelity*), thus lessening the costs associated with relocating. A generalist strategy may also prevent competition with African resident species. Although competition with resident species does occur, such behaviour is thought to be relatively uncommon (Salewski et al., 2007 and references therein), and so interspecific competition may not be a significant reason for a adopting a generalist wintering strategy.

Evidence suggests that a generalist wintering strategy is relatively common amongst long-distance migrants. For other species, including whinchats, much accessible and suitable habitat remains unoccupied during winter (Cresswell et al., 2007; Hulme and Cresswell, 2012; Wilson and Cresswell, 2006), individuals are not restricted to optimal sites (Greenberg, 1992; Hutto, 1988; Karr, 1976; Lynch, 1992; Waide, 1980), and winter territories often span a wide range of habitat types of varying quality, including sub-optimal habitats (Jones et al., 1996b; Karr, 1976; Leisler, 1990; Marra and Holmes, 2001; Petit et al., 1999; Rabøl, 1987; Salewski and Jones, 2006). Consequently, many other migrants are also suggested to be winter habitat generalists (Hutto, 1992; Marra and Holmes, 2001; Rappole and McDonald, 1994; Stiles, 1980). For example, migrating blackcaps occupy more diverse habitats than resident species, suggesting a more generalist strategy in the non-breeding season (Pérez-Tris and Tellería, 2002). Some species, however, have adjusted their migratory behaviour in response to changing conditions in the short-term,

suggesting less flexibility to changing conditions (Sutherland, 1998 and references therein), but it is unclear whether this is driven by more specialist requirements during summer or winter. The absence of breeding pressures and constraints may allow a non-specialist winter strategy, even if species are specialists during breeding. Along with our findings, whinchats have been shown to be associated with a wide range of vegetation characteristics in some breeding areas (Pearce-Higgins and Grant, 2006), suggesting generalist habitat requirements also during the breeding season. Further work is needed to quantify the differences or similarities in the degree of specialism between the breeding and non-breeding seasons.

Lack of dominance-based habitat occupancy

We found no evidence for habitat-based habitat occupancy during winter. Neither habitat characteristics within territories or territory size differed according to age or sex. Data are sparse for the Palearctic system (Catry et al., 2004a; Vickery et al., 2014), although winter habitat segregation between the sexes has been shown for red-backed shrikes *Lanius collurio* in Botswana (Herremans, 1997) and eastern great reed warblers *Acrocephalus orientalis* in Malaysia (Nisbet and Medway, 1972). Wintering blackcaps *Slyvia atricapilla* show no habitat segregation according to sex, but juvenile birds are more likely to be found in poorer quality habitats (Pérez-Tris and Tellería, 2002). On the wintering grounds in Iberia, European robins *Erithacus rubetra* exhibit habitat segregation according to age, sex and body size, in which subordinate juveniles and females are found in poorer quality habitats and have lower body condition as a result (Catry et al., 2004a). There is also some evidence for altitudinal segregation in wintering snow buntings (Smith et al., 1993). Also in contrast to our findings, many Neotropical migrants exhibit dominance-based habitat segregation on the wintering grounds, such as American redstarts *Setophaga ruticilla* (Marra, 2000; Parrish and Sherry, 1994), prairie warblers *Setophaga discolour* (Latta and Faaborg, 2001), hooded warblers *Setophaga citrina* (Lynch et al., 1985; Morton, 1990; Stutchbury, 1994) and black-throated blue warblers *Setophaga caerulescens* (Wunderle Jr, 1995), amongst others (Ornat and Greenberg, 1990), and these differences often lead to differential survival and reproductive success (Marra

and Holmes, 2001; Reudink et al., 2009). In some wintering areas, however, there is an absence of habitat segregation for both American redstarts and black-throated blue warblers (Holmes et al., 1989), suggesting that the degree of segregation may be population or habitat-specific. As per our results, a lack of dominance-based habitat segregation and no influence of age and sex on territory size has been shown for willow flycatchers *Empidonax traillii* wintering in Costa Rica (Koronkiewicz et al., 2006), and for wintering prothonatory warblers *Protonotaria citrea* (Ornat and Greenberg, 1990). For whinchats, non-specialist wintering requirements would mean that a large number of habitat types could provide territories of sufficient quality, and it is also likely that any winter territory that allows survival is adequate for territory establishment. Thus the need for competition between conspecifics for territories of varying quality is removed. Further research on other species is needed to determine whether the lack of dominance-based habitat occupancy seen here for whinchats is either uncharacteristic or common of the Palearctic system.

The difference in the degree of dominance-based segregation between different migrants, for example the seemingly greater occurrence of segregation in the Neotropics, is perhaps explained by a lower availability of suitable habitat during the non-breeding season in those areas. If winter habitat availability is limited, as is suggested to be the case for Neotropical migrants (Rappole et al., 2003; Rappole and McDonald, 1994; Sherry and Holmes, 1996), we would expect there to be more competition for limited territories. Alternatively, species that exhibit dominance-based habitat occupancy may have more specialist requirements, which may limit the amount of suitable wintering habitats and lead to competition between conspecifics. What is clear is that more research is needed to determine any links between the degree of habitat specialism and dominance-based habitat segregation.

Predictors of territory size and space use within territories

The influence of habitat characteristics associated with shrub density on both territory size and space use within territories suggest that perches are an important feature of wintering territories. Individuals had larger territories if shrubs were

sparser and maize was absent within the territory, and more frequently used areas of their territories that had significantly more perching shrubs. For whinchats, perching shrubs and structural vegetation diversity are important features within breeding territories (Fischer et al., 2012; Horch and Birrer, 2011), stopovers sites (Koce and Denac, 2010), and on the wintering grounds (Barshep et al., 2012; Hulme and Cresswell, 2012), and an absence of perches has been shown to significantly influence habitat selection during breeding (Bastian and Bastian, 1996; Labhardt, 1988; Oppermann, 1990). Koce and Denac (2009) identified perches as the most important feature of habitat selection during stopovers. Perches are most likely a key component of winter habitat because of their importance for effective foraging and territory defence (Fischer et al., 2012 and references therein), and the influence of both perching shrubs and maize crops on territory size suggests that there is a threshold regarding the number of perches needed for a territory to be suitable. Despite significant changes in other habitat characteristics over winter, shrub density remained unchanged throughout, most likely allowing individuals to remain in their wintering territories and further highlighting the importance of perching shrubs for winter territory establishment. Whilst our results do show that perches are a necessary aspect of winter territories, what structure provides a perch is non-specific. Given the abundance of both natural and artificial structures within anthropogenically-modified open savannah, a requirement for perches still allows for generalist habitat preferences within the wintering range.

Resilience to winter habitat degradation

Our results suggest that whinchats may have some population resilience to anthropogenic habitat degradation. A lack of dominance-based habitat occupancy with either age or sex, for example, would prevent skewed population dynamics should a particular habitat type become unsuitable or degrade faster than others and cause higher mortality for a particular age or sex class. If high quality individuals occupy both poor and high quality habitats, and also a range of habitat types (as is implied by our finding that body condition does not predict territory habitat characteristics), high quality individuals would still survive even under

disproportional loss of one habitat type. Most territories had some level of human disturbance, chopping and some active farmland, and whinchats established territories in grazed areas, suggesting some tolerance to human-modified habitats. Some human activities, such as chopping for wood harvesting, farming and grazing, may provide more suitable perches or foraging opportunities. Whinchats did not move territories despite an increase in grazing intensity over winter. That shrub density remained unchanged suggests that grazing does not influence those habitat features crucial to winter territories. Instead, grazing most likely leads to an increase in bare ground (as was indeed seen over winter), which provides foraging opportunities for ground foraging insectivorous birds such as whinchats and may therefore be beneficial (Schaub et al., 2010). Maize crops in particular appear to be well tolerated, implying that some human-modified habitats may provide high quality wintering habitats. Maize comprised over half of a typical territory plot if it was present, and significantly reduced territory size, suggesting that this land type provides more resources per area. Similar to our findings, Hulme and Cresswell (2012) found that whinchats were more likely to occur in crops with structural characteristics, including maize. Considering the importance of perching shrubs within winter territories, maize is probably beneficial because it provides more perching structures above bare ground. Nevertheless, sample sizes are relatively low for exploring the influence of maize so these conclusions should be taken conservatively.

In summary, our study is one of the first to document winter habitat use at the territory-scale for a Palearctic migrant. We demonstrate that whinchats are winter habitat generalists within their wintering habitat of open savannah and show no dominance-based habitat occupancy during winter. Generalist habitat requirements and a preference for few key habitat characteristics likely promote flexibility both within and between winters and so may engender population resilience to habitat change and degradation. Whinchats may thus show resilience to anthropogenic habitat modification and may even benefit from an increase in farming in the region, and therefore some resilience to the rapid anthropogenic habitat degradation occurring in Africa.

CHAPTER 5. HIGH OVERWINTER AND ANNUAL SURVIVAL FOR A DECLINING PALEARCTIC MIGRANT: EVIDENCE THAT WINTERING CONDITIONS MAY NOT LIMIT MIGRANT POPULATIONS

5.1 Abstract

Accurately measuring true annual and overwinter survival rates of migrants, identifying which factors influence their survival, determining whether survival varies across age and sex classes, and ultimately establishing whether overwinter survival is a major component of annual survival is fundamental to understanding population dynamics and so for the conservation of migrants. Despite this, data are scarce, especially from the wintering perspective. This study is one of the first to document annual and overwinter survival from the wintering grounds for a declining Palearctic migrant, the whinchat. We monitored a population of marked individuals for which dispersal was low and detectability was high, allowing for estimates of true survival. We explored whether annual and overwinter survival differed with age and sex and whether aspects of wintering ecology such as winter habitat and residency time in the previous winter influenced annual survival. Annual survival was at least 52% and did not differ significantly between age and sex classes or with either habitat characteristics or residency time in the previous winter. Overwinter survival was very high: monthly survival was at least 98% at some study sites. Residency during winter differed across sites, but lower residency did not correlate with reduced annual survival, suggesting the occupancy of multiple wintering sites rather than higher winter mortality. Our results suggest that mortality occurs primarily outside of the wintering period, most likely during migration, and that influence of winter conditions on survival is minimal. The similarity between survival rates for all age and sex classes when measured on the wintering grounds implies that any difference in survival with age or sex occurs during the first migration or during the post-fledging stage, and suggests that migrants have a generalist migratory strategy. Our findings suggest that the wintering grounds do not limit populations as much as the

migratory and breeding stages, which is likely a key finding for the conservation of migrants.

5.2 Introduction

Migrant birds are affected by conditions both in the breeding and non-breeding seasons, both of which have a strong influence on life history traits and therefore population dynamics (Moore et al., 1995; Newton, 2010a). Species breeding in temperate areas may migrate to take advantage of reduced competition, lower predation, seasonal increases in food resources and increased day length at higher latitudes for breeding (Alerstam et al., 2003; Alerstam and Högstedt, 1982; Cox, 1968; Lank et al., 2003), and return to their wintering areas when the costs of less optimal abiotic conditions, less abundant resources and less suitable habitat become limiting (Levey and Stiles, 1992).

Differing constraints and pressures on the breeding and wintering grounds and those during the migratory journey mean that each stage has costs and implications for survival. Higher abiotic pressures and the costs of reproduction may result in lower survival on the breeding grounds compared to winter (Newton, 2010a). Mortality can occur during migration itself due to unpredictable weather conditions, degradation or loss of stopover sites, or navigational errors (Newton, 2010a, 2006b). Consequently, mortality rates may be higher when compared to sedentary periods, due primarily to the huge energetic costs and unpredictability of migratory flight (Newton, 2006b; Sillett and Holmes, 2002). Survival may differ between migratory journeys because the costs and carry-over effects of breeding and wintering differ, and migration strategy often differs between spring and autumn (Newton, 2010a). Although survival may be higher during winter, winter habitat affects body condition (Ottosson et al., 2005; Strong and Sherry, 2000), which impacts departure dates (Saino et al., 2004; Studds and Marra, 2005), condition during migration (Bearhop et al., 2004) and migration speed (Tøttrup et al., 2008), which ultimately influence survival during migration, the timing of arrival on the breeding grounds and future breeding success (Aebischer et al., 1996; Kokko, 1999; Møller, 1994; Norris et al.,

2004; Potti, 1998; Saino et al., 2004; Smith and Moore, 2005). On the breeding grounds, the costs of reproduction, predation from increased activity during breeding, habitat loss and abiotic pressures are all likely to influence subsequent parts of the life cycle (Inger et al., 2010; Norris, 2005). Consequently, each stage often has carry-over effects throughout the annual cycle and consequences for future survival and reproduction (González-Prieto and Hobson, 2013; Inger et al., 2010; Marra et al., 1998; Marra and Holmes, 2001; Newton, 2010a, 2004; Norris, 2005; Norris and Marra, 2007; Reudink et al., 2009; Rockwell, 2013; Sherry and Holmes, 1996; Studds and Marra, 2005; Webster et al., 2002). Whether winter conditions are more influential on survival that breeding conditions is likely to be both species and population-specific (Sherry and Holmes, 1995).

Survival rates during the different stages of the annual migratory cycle are likely to vary between demographic groups because annual strategies and the factors influencing survival often vary with age and sex. Overwinter survival may be lower for birds in their first winter because the chance of arriving in poorer habitats is greater due to the predicted stochastic nature of the first migration, for example (Cresswell, 2014), and mortality during migration is likely to be higher for inexperienced individuals. As a result, annual survival is often lower for first year birds than adults (Dugger et al., 2004). Survival may differ between males and females if migration behaviour differs between the sexes (Ketterson and Nolan Jr, 1983). Breeding costs are often higher for inexperienced first-time breeders and for females over males (Hanssen et al., 2005; Viallefont et al., 1995), and this may influence the number of individuals returning to the wintering grounds. Juveniles often have lower breeding success as a result of differences in migratory phenology compared to adults (McKinnon et al., 2014 and references therein). For species with low site fidelity, dominance-based habitat occupancy on the breeding and wintering grounds can force less dominant individuals into poorer habitats (Catry et al., 2004a; Figuerola et al., 2001; Lynch et al., 1985; Marra and Holmes, 2001; Parrish and Sherry, 1994). Individuals residing in poor habitats often have reduced survival (Jones et al., 1996b; Marra and Holmes, 2001; Norris et al., 2004; Rappole et al., 1989; Robbins et al., 1989), and this has implications at the population level if less

dominant demographic classes have lower survival and population dynamics become skewed. Alternatively, if migrants are non-specialist and can tolerate a wide range of relatively poor wintering habitats (e.g. see Cresswell, 2014) then it is unlikely that survival will vary with age or sex during the winter. Generalist requirements allow many migrants to be highly site faithful after completing one successful migration (see Chapter 3: *Site fidelity*), suggesting that survival is likely to be similar between adults and juveniles upon reaching the wintering grounds.

Survival must be measured during and between different migratory stages and for different demographic groups in order to best derive where mortality is occurring during the annual cycle. Survival during migration can be established if annual survival is known from both breeding and wintering areas. For example, if survival is lower only during the first migratory flight from Europe to Africa, then annual survival rates should differ between first-winter and adult birds on the breeding grounds, but not on the wintering grounds. Combining estimates of survival or residency during one stage with annual survival for those individuals can also identify whether a reduction in the number of resident individuals is due to increased mortality or dispersal outside of the study area. Accurate survival estimates for each stage of the annual cycle are therefore essential for understanding population trends and so for the conservation of migrants, many of which are declining (Sanderson et al., 2006; Vickery et al., 2014). Despite the importance of accurate survival estimates, data are scarce, especially for the wintering period (Grüebler et al., 2014).

Key to estimating survival at any stage is knowledge of the degree of site fidelity and the ability to distinguish between survival and dispersal. Annual survival estimated from return rates is often lower than true survival (Ergon and Gardner, 2013; Gilroy et al., 2012; Schaub and Royle, 2013) because individuals disperse; yet if individuals are highly site-faithful and the ability to detect any dispersal is high, it may be possible to estimate 'true' survival as opposed to 'apparent survival'. Apparent survival is mostly a function of the scale of monitoring and so is less valuable for population management (Anders and Marshall, 2005; Ergon and Gardner, 2013; Gilroy et al., 2012; Schaub and Royle, 2013).

Here we estimate annual survival and overwinter survival, differentiate between long-range dispersal and mortality during winter, and explore age, sex and habitat effects on survival for a population of a declining Palearctic migrant, the whinchat on its wintering grounds in West Africa. We have shown that apparent survival likely reflects true survival for this study population due to high detection probability and extremely high site fidelity at the territory-level (see Chapter 3: *Site fidelity*). As a small passerine migrant, whinchats are likely to have a wintering strategy driven by stochastic site selection within the wintering range by juveniles in their first winter, high site fidelity for surviving adults in subsequent winters, and generalist ecological requirements (the serial residency hypothesis: Cresswell, 2014: see Chapter 3: *Site fidelity* and Chapter 4: *Winter habitat*). Here, we present annual survival estimates as true survival and not apparent survival. We ask:

1. What are annual survival rates?
    - Do return rates differ with age and sex, between winters or between wintering sites?
    - Do habitat characteristics in the previous winter influence return rates?

2. Does winter residency time vary across sites, with age and sex, and between birds that returned and did not return in the following year?

3. What are overwinter survival rates?
    - Does overwinter survival differ with age and sex?

We predict that annual survival will be high and similar to that reported on the breeding grounds because we expect most mortality to occur during migration. We expect annual survival to be lower for first year birds due to their inexperience during spring migration and also on the breeding grounds as first-time breeders. We predict overwinter survival to be high because ecological constraints and the pressures of the breeding season are largely absent during winter, all wintering birds have already migrated successfully from the breeding grounds, and a non-specialist

wintering strategy promotes survival under a wide range of conditions. We predict no age and sex differences in overwinter survival and no influence of winter habitat because of generalist requirements and previous findings of no dominance-based habitat occupancy on the wintering grounds (see Chapter 4: *Winter habitat*).

5.3 Methods

For details of study sites, resighting protocol, and calculating territory size, refer to Chapter 2: *General methodology*. For details of habitat methodology and analyses, see methods in Chapter 4: *Winter habitat*.

Sample sizes

For the following results and analyses, data are presented for 154 birds ringed across winters 1 and 2 and resighted at least once after capture (winter 1 = 38, winter 2 = 116). Birds fitted with geolocators and those ringed at sites J and H in winter 2 (*n* = 58 winter 2, *n* = 130 winter 3) are excluded, because the influence of geolocators on the survival of whinchats is unknown, and it was not certain whether individuals ringed at the end of winter 2 were resident or transient, both of which may bias survival estimates. Birds which could not be confidently aged or sexed were excluded from models including age and sex as predictors. All individuals ringed in winter 3 are excluded because return rates are unknown and overwinter survival was not thoroughly explored in this study winter. One individual was excluded from habitat analyses because its territory was in an unrepresentative habitat (dense coffee farm), which grossly inflated the vegetation counts within that territory. Nonetheless, removing this individual did not change any main findings.

Statistical analyses

'Residency' was defined as the amount of time in which an individual was known to be present at the study site. To test whether annual survival differed between birds with short and long residency periods in the previous winter, we defined short

residency as being present until 19th January – the middle of the resighting period and loosely half the wintering period – and long residency as presence after this date, and used paired Wilcoxon tests. When exploring overwinter survival, we focussed on birds from a single site (site A) because winter residency time differed between study sites but residency time did not predict annual survival (see following results). Here, a larger number of individuals were followed and ringed (n = 32 followed for this study), and winter residency was high, allowing us to document and explore predictors of survival. We included birds captured or seen at this site in winter 2 before 1st January for overwinter survival analyses. Generalised Linear Models (logistic regression) were used to test predictors of both overwinter and annual survival. We used short or long residency (as defined above) when exploring predictors of return rates. When modelling the influence of age and sex on survival, we included all birds of known age and sex across all sites because age and sex ratios were the same across sites.

Analyses were performed in R version 3.0.1 (R Development Core Team, 2013) and RStudio Version 0.98.507. Data were checked for normality and for multicollinearity using variance inflation factors (CARS package; Fox and Weisberg, 2010) and non-parametric tests were used when necessary. Multiple regression model simplification was based on Akaike Information Criterion (AIC) (Bozdogan, 1987), where variables failing to improve AIC or significantly contribute to the model (as determined by a non-significant ANOVA results performed between models) were removed from the model. For models of the same or similar sample sizes across all variables, a dredge analysis was used to identify minimal adequate models (Bartoń, 2012): cases with missing values were removed from the dataset as required, and resulting minimal adequate models were produced using complete datasets. When presenting top models from dredge analyses, we presented models within three AICc of the top model as this gave an adequate sample of models. For all candidate final models, model fit was evaluated from diagnostic model plots and models presented if assumptions were reasonably met (Crawley, 2007). Mean values are ± one standard error. A statistical significance level of p <0.05 was chosen to reject null hypotheses.

5.4 Results

1. Annual survival

Annual survival was at least 52% (Figure 5.1; Table 5.1). 54% of individuals seen in winters 1 and 2 returned to the study area in the following winter (Table 5.1). Return rates did not differ with age, sex, site or winter (study year), or with whether a bird had a long or short residency period in the previous winter (Figures 5.1 and 5.2; Tables 5.2 and 5.3; plus see following results).

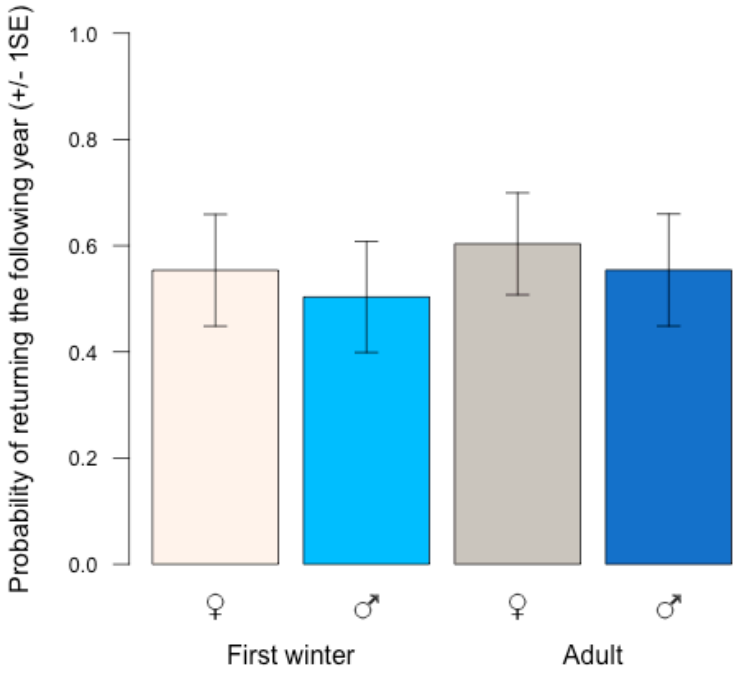


Figure 5.1. Return rates did not differ with age and sex. Predicted values for probability of return in following winter according to age and sex (± SE) from the logistic regression analysis: returned next year ~ age + sex (see Table 5.3; *n* = 94). Birds from winter 1 that returned in both winters 2 and 3 are included in return rates for winter 2 only.

Table 5.1 Numbers of birds involved in the study and resighted (RS) at least once after capture, separated by age and winter (W). All birds fitted with geolocators and those ringed at sites J and H in winter 2 are not included in the totals because their residency, return status and any influence of geolocator fitting was unknown (*n* = 58 winter 2, *n* = 130 winter 3; see methods). Figures are number of individuals, plus percentage of the total individuals in that age category (first-winter and adult columns) or of all individuals for that row (study total column) in brackets. Birds of unknown age (*n* = 1 winter 1, *n* = 2 winter 2) are excluded from age-specific totals but not from study total. In four cases a bird was only resighted the following winter (*n* = 2 winter 1, *n* = 2 winter 2). Ages of 'returned' and 'not returned' birds are those of the previous year. First-winter birds from winter 1 are included in adult totals for following years and are included in winter 3 return rates if they returned in winter 2.

	First-winter			***Adult***			***Study total***		
	ΣRS	Returned	Not returned	ΣRS	Returned	Not returned	ΣRS (+U age)	Returned	Not returned
Winter 1	12 (33%)	-	-	24 (67%)	-	-	36 (1)	-	-
Winter 2									
W1 birds	-	6 (50%)	6 (50%)	-	15 (62.5%)	9 (37.5%)	21 (0)	21 (58%)	15 (42%)
Newly ringed	33 (54%)	-	-	28 (46%)	-	-	61 (2)	-	-
Winter 3									
W1 birds	-	-	-	-	-	-	-	9 (24%)	28 (76%)
W1 returned in W2	-	-	-	-	-	-	-	9 (43%)	12 (57%)
All known from W2	-	19 (58%)	14 (42%)	-	23 (47%)	26 (53%)	82 (2)	44 (52%)	40 (48%)
Birds ringed in W2	-	19 (58%)	14 (42%)	-	14 (50%)	14 (50%)	63 (2)	33 (54%)	28 (46%)
Newly ringed	48 (51%)			46 (49%)			94 (0)		
Total	101 (49.5%)	29 (56%)	23 (44%)	103 (50.5%)	38 (50%)	38 (50%)	196 (3)	**65 (54%)**	**56 (46%)**

Habitat variables within a bird's territory in the previous winter had no influence on the probability of it returning in the following year (Table 5.4), including those habitat variables found to influence territory size (presence of maize and territory shrub score; Figure 5.3.

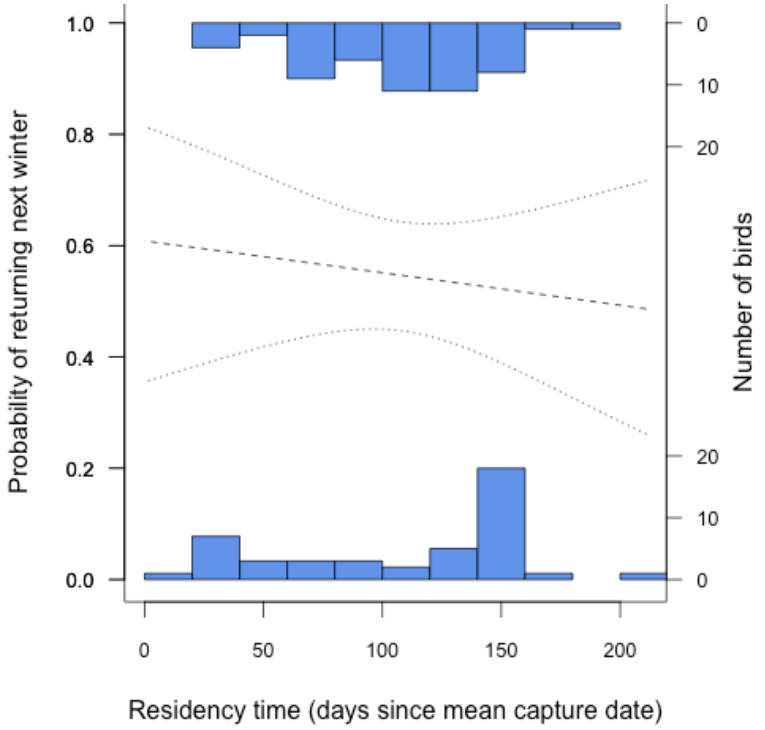


Figure 5.2. The probability of a bird returning next winter in relation to its residency time in the previous winter – note the relationship was NOT significant. Histograms show residency period for birds that returned (top bars) or did not return (lower bars). Predicted values (dashed line, ± SE (dotted lines)) are plotted from an individual logistic regression model of returned ~ residency time (estimate = -0.0023, SE = 0.0045, z = -0.5, p = 0.60, Residual deviance for model = 133.4 on 95 df, AIC = 137.4, n = 97).

Table 5.2. The top nine models (within 3 AICc of the top model*) of all possible models exploring predictors of annual return rates, from the initial maximal model of: returned next year ~ age + sex + size + winter (study year) + site + residency time (short or long) + age*site + sex*site + age*sex + site*residency time. All terms, including interaction terms were NS. The null model was the top minimal adequate model; n = 86.

Component	Log Likelihood	AICc	ΔAICc	Weight
Null	-59.40	120.85	0.00	0.25
Age	-58.91	121.97	1.12	0.15
Winter	-59.08	122.30	1.45	0.12
Sex	-59.35	122.85	2.00	0.09
Residency time	-59.35	122.85	2.00	0.09
Size	-59.39	122.92	2.07	0.09
Site	-58.49	123.27	2.42	0.08
Age + winter	-58.69	123.68	2.83	0.06
Residency time + winter	-58.71	123.70	2.85	0.06

* 3 AIC chosen to give a representative number of top models

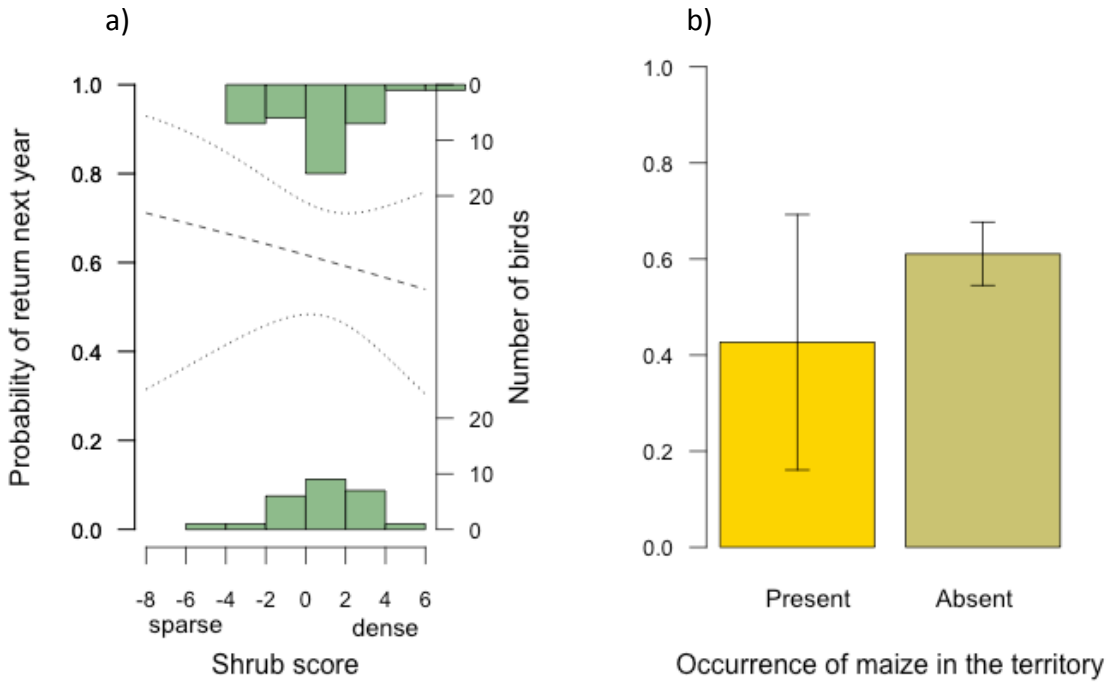


Figure 5.3. The probability of a bird returning next winter as a result of a) the density of perching shrubs ('shrub score') and b) whether maize was present within the territory in the previous winter. For a), predicted values (dashed line, ± S.E. (dotted lines)) are plotted from a logistic regression model of returned ~ shrub density (estimate = 0.045, S.E. = 0.36, z = 0.7, *p* = 0.47, Residual deviance for model = 43.9 on 31 df, AIC = 47.8, *n* = 32). Values for b) are predicted from a logistic regression of returned ~ presence of maize + shrub score, using medium values for shrub score. Note – the relationship and difference are both NOT significant.

Table 5.3. Results from logistic regression analyses exploring predictors of return rates. The first model (initial maximal model of: returned next year ~ age + sex + size + winter (study year) + site + residency time (short or long) + age*site + sex*site + age*sex + site*residency time) is presented as the results from averaging the top nine models (within 3 AICc of the top model*, Table 5.2). The null model was the top model: all terms were NS. The model of returned next year ~ age + sex used to predict return rates for Figure 5.2 is also presented, in which both predictors are NS (residual deviance = 128.9 on 91 df; AIC = 134.9). Note that site A and age = adult are the reference categories; *n* = 86 for full model, *n* = 94 for model of returned ~ age + sex.

	Full model		All models ΔAICc < 3			Model of returned ~ age + sex			
Variable	*z*	*p*	Model-averaged parameter estimate	SE	Relative weight	Parameter estimate	SE	*z*	*p*
(Intercept)	0.6	0.54	0.23	0.44		0.42	0.43	1.0	0.32
Age FW	0.9	0.35	-0.42	0.44	0.21	-0.20	0.44	-0.5	0.65
Winter 2	0.8	0.41	-0.40	0.48	0.25	-0.20	0.44	-0.5	0.65
Sex male	0.3	0.76	0.20	0.44	0.09				
Residency	0.5	0.61	-0.0028	0.0052	0.15				
Size	0.2	0.88	-0.048	0.32	0.09				
Site B	0.7	0.47	0.38	0.52	0.08				
Site JF	0.8	0.40	-0.49	0.58					

* 3 AIC chosen to give a representative number of top models

2. Winter residency

Across resident birds (i.e. those seen at least 30 days after capture), overwinter residency periods varied between sites (Table 5.5, Figure 5.4). Across all sites, residency time did not differ with age or sex (Table 5.5). If the cumulative number of days a bird was recorded at a site is a function of survival rather than adaptive variation in residency time, we should see a relationship between annual survival and residency period: this was not the case. Whether residency period was short or long did not differ between birds that returned or did not return in the following year (Wilcoxon rank sum test with continuity correction: $W = 862.5$, $p = 0.99$, $n = 97$; Figures 5.2 & 5.4).

Table 5.4. Results from logistic regression analyses exploring the influence of habitat on the probability of return in the following year. The full model (Generalised Mixed Model of: returned next year ~ presence of maize + percentage of farm + level of grazing + plant diversity + shrub density + vegetation clumping + vegetation cover + age + sex + size at capture + (1|site)) is presented as the results from a dredge analysis averaging all 33 models within 3 AICc of the top model*. The null model was the top model (all terms NS). Note that the reference categories are sex = female, age = adult; *n* = 57)

	Full model		All models ΔAICc < 3		
Variable	*z*	*p*	Model-averaged parameter estimate	SE	Relative weight
(Intercept)	1.1	0.27	0.83	0.75	
Vegetation cover	1.3	0.19	-0.44	0.34	0.41
Sex male	1.2	0.22	-0.74	0.60	0.27
Age first-winter	1.1	0.26	-0.68	0.60	0.24
Grazing	0.9	0.34	-0.52	0.55	0.17
Plant diversity	0.9	0.39	-0.57	0.66	0.13
Shrub density	0.7	0.50	-0.087	0.13	0.13
Vegetation clumping	0.4	0.66	0.12	0.27	0.07
% Farm	0.3	0.75	-0.0037	0.012	0.05
Presence of maize	0.3	0.78	-0.29	1.0	0.05
Size at capture	0.3	0.74	-0.13	0.38	0.05

* 3 AIC chosen to give a representative number of top models

Table 5.5. Results from multiple regression analyses exploring differences in residency period with age and sex and across sites. The full model is: residency time (last day resighted) ~ site + age + sex. Residency differed across sites (age and sex terms NS, Residual standard error for full model = 45.3 on 109 df, $F_{6,109}$ = 13.2, Adjusted R^2 = 0.39, *p* = <0.001). Note that site A and adult female are the reference categories; *n* = 116.

Component	Parameter estimate	SE	*t*	*p*
Intercept	111.8	10.45	10.7	<0.001
Site B	-22.8	11.82	-1.9	0.057
Site H	-84.4	12.77	-6.6	<0.001
Site J	-92.1	13.82	-6.7	<0.001
Site JF	-52.1	13.05	-4.0	<0.001
Age F	-13.3	8.92	-1.5	0.14
Sex M	6.5	8.95	0.7	0.47

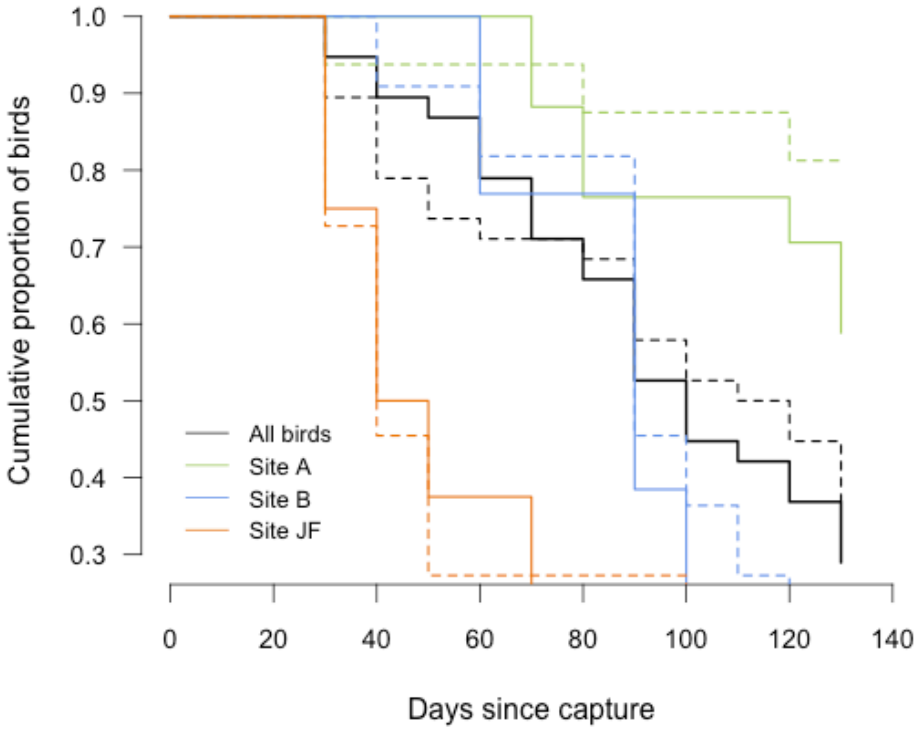


Figure 5.4. The proportion of resident birds (i.e. sighted at least 30 days after capture) known to be alive at all study sites in days since capture in winter 2, based on resightings in winter 2, separated by site. The black line shows data for all birds across all sites. Solid lines are birds that returned to the study site in the following winter (i.e. certain to be alive even if not resighted after day n = 1); dashed lines are birds that failed to return in the following winter. Birds returning to the study site from winter 1 were given a capture date of 25th September (the start of monitoring in winter 2). If cumulative probability of occurrence was related to survival rather than residency we would expect a significant difference between the dashed and solid lines for a site (colour of line). Sample sizes: Site A n = 33, Site B n = 24, Site JF n = 19.

3. Overwinter survival

At site A, for birds that were resident for at least 30 days after capture, 100% were still alive after the minimum amount of time that any bird returning in the following year was resident (60 days across all sites, n = 32, Figure 5.4). At site A, 84% (27/32) of birds were resighted at least 90 days after capture and 78% (25/32) were resighted at least 120 days after capture; when accounting for whether missing

individuals returned in the following year, 97% (31/32) of birds survived at least 90 days after capture and 94% (30/32) survived at least 120 days after capture (Figure 5.4). This is equivalent to an average monthly overwinter survival rate of 98%. If it is assumed that all birds were present at the wintering grounds on 1st October when all individuals were likely to have arrived and accounting for whether missing individuals returned in the following year, 100% individuals were present 90 days after arrival and 97% (31/32) were present at 120 days after arrival (Figure 5.4). This equates to a monthly survival rate of 99% on the wintering grounds.

Overwinter survival did not differ with age or sex (age: $F_{1,28} = 0.02$, $p = 0.90$; sex: $F_{1,28} = 0.5$, $p = 0.50$; $n = 31$).

5.5 Discussion

Annual survival

Annual survival was at least 52%, and 54% over the two study years, a figure we are confident reflects true survival because of our ability to detect dispersing birds coupled with the high site fidelity of whinchats (see Chapter 3: *Site fidelity*). Our figures are similar to or higher than annual survival rates reported in a study of 12 species of Palearctic migrants wintering at a site in the Gambia (King and Hutchinson, 2001), and similar to between-winter return rates for Neotropical migrants such as American redstarts *Setophaga ruticilla* (0.44), black and white warblers *Mniotilta varia* (0.42) and black-throated blue warblers *Setophaga caerulescens* (0.58) (Wunderle Jr and Latta, 2000). In Jamaica, Holmes and Sherry (1992) report similar return rates of 51% for American redstarts and 46% for black-throated blue warblers (Holmes and Sherry 1992). A study on willow flycatchers *Empidonax traillii* found annual return rates of 68%, higher than presented here for whinchats (Koronkiewicz et al., 2006). Compared to return rates on the breeding grounds, our figures are higher than those documented for whinchats (return rates of 11 – 47% and annual mortality rates of 55-66% (Bastian, 1992; Bezzel and Stiel, 1977; Schmidt and Hantge, 1954)), and similar or higher than return and survival

rates reported for other site-faithful Palearctic migrants (great reed warbler *Acrocephalus arundinaceus*: return rate of 55% (Bensch and Hasselquist, 1991); barn swallow *Hirundo rustica*: survival estimates of 0.36 – 0.42 (Møller and Szép, 2005; Robinson et al., 2008); sand martin *Riparia riparia*: survival estimates of 0.29 – 0.31 (Cowley and Siriwardena, 2005; Robinson et al., 2008); common house martin *Delichon urbicum*: survival estimate of 0.42 (Robinson et al., 2008)), and also many Neotropical migrants (Desante et al., 1995), such as return rates of 41 (±7%) and annual survival estimates of 0.52 (±0.07) reported for ovenbirds *Seiurus aurocapilla* (Porneluzi and Faaborg, 1999). Lower annual survival rates of 0.25 – 0.42 are reported for some Neotropical migrants (Conway et al., 1995).

Higher return rates on the wintering than those reported on the breeding grounds suggests either 1) higher survival outside of the wintering season, 2) higher mortality immediately after breeding or on the route to the wintering grounds, or 3) higher dispersal (and a failure to detect such dispersal) of adults and juveniles on the breeding grounds than any dispersal during winter, or a combination of the above. Breeding dispersal has indeed been documented in whinchats, and dispersal rates are higher for returning juveniles than adults (Bastian, 1992; Bezzel and Stiel, 1977; Shitikov et al., 2012). Our annual survival rates may be higher because they were not confounded by dispersal, as may often the case when estimating survival on the breeding grounds (Marshall et al., 2004).

Overwinter survival

Overwinter survival was very high, as predicted, with an average monthly survival rate of 98% for birds at site A. This increased to 99% when accounting for individuals that departed sites early but returned in the following year. Overwinter survival estimates for other migrants are scarce (Holmes et al., 1989), especially habitat-specific estimates (Conway et al., 1995) and for Palearctic migrants. In the Neotropics, very high overwinter survival has been documented for black-throated blue warblers (Sillett and Holmes, 2002) with estimates of up to 0.99 (Holmes, 2007). Holmes *et al* (1989) report 80% overwinter survival for American redstarts and 66%

for black-throated blue warblers. High overwinter survival of 80-92% is reported for willow flycatchers (Koronkiewicz et al., 2006). For whinchats, generalist habitat requirements within open savannah (see Chapter 4: *Winter habitat*), combined with reduced abiotic constraints, predation and pressures compared to breeding, are all likely explanations for such high survival during winter. This likely explains why individuals spend most time on the wintering grounds (see Chapter 6: *Migration*).

Age and sex differences

We found no age or sex differences in either annual or overwinter survival. Similar overwinter survival between juveniles and adults is reported for barn swallows (Grüebler et al., 2014), prothonotary warblers *Protonotaria citrea* and northern waterthrushes *Parkesia noveboracensis* (Calvert et al., 2010). Similar survival rates between sexes are reported for black-throated blue warblers (Sillett and Holmes, 2002), although Holmes *et al* (1989) present evidence for lower overwinter survival for first-winter birds of both this species and American redstarts. Overwinter survival is also lower for first-winter ovenbirds and first-winter black-and-white warblers (Dugger et al., 2004). Annual survival may be lower for male willow flycatchers compared to females (Koronkiewicz et al., 2006). Apart from suggesting no true difference in survival between age classes, similar survival between first-winter and adults suggests that any age-related variation in survival occurs during the first migratory journey between Europe and the wintering grounds. Similar survival between the sexes suggests that the pressures of breeding and migrating are similar for males and females, or that any differential survival for one sex is counteracted with lower survival for the other during another part of the annual cycle. For whinchats, female mortality is reported to be higher that males on the breeding grounds (Grüebler et al., 2008).

Influence of winter habitat on survival

We found no evidence of winter habitat influencing annual survival. No influence of habitat on survival has been documented in several Neotropical migrants when

comparing mature and successional forests (Conway et al., 1995), although the authors of this study suggest that they were not able to detect large differences. More commonly, for Neotropical migrants where this has been studied, survival is indeed linked to winter habitat, especially in relation to the age and sex of individuals, as sub-ordinate individuals are forced into poorer quality habitats (Sherry and Holmes, 1996 and references therein). In contrast, our findings support a lack of dominance-based habitat occupancy on the wintering grounds (see Chapter 4: *Winter habitat*) and instead support generalist wintering requirements (Cresswell, 2014). The ability of whinchats to use a wide range of ecological conditions and habitat characteristics within open savannah most likely allows high overwinter survival even in apparently sub-optimal habitats and reduces any carry-over effects of winter habitat on subsequent survival and possibly also reproduction. If winter habitat does indeed influence annual survival, for example by limiting subsequent pre-migratory fattening that is necessary to survive migration, it may be that individuals compensate by moving to higher quality wintering sites immediately before migrating. If this were the case, we would not expect to find differences in annual survival based on winter territory habitat characteristics.

Where is mortality occurring?

Combining results of annual and overwinter survival with studies exploring age, sex and habitat effects enables us to hypothesise where mortality may be occurring in the annual cycle. Our higher estimate of annual survival to those reported on the breeding grounds, very high overwinter survival, and no age or sex differences in either annual or overwinter survival strongly suggests that mortality is greatest during the post-fledging period and during the first migratory journey to the wintering grounds. This is particularly likely considering that first year migrants are often reported to have lower annual survival when measured on the breeding grounds (Dugger et al., 2004). Post-fledging survival is often low for juvenile whinchats, especially in managed grasslands (Müller et al., 2005; Tome and Denac, 2012) where breeding populations have been severely affected by agricultural intensification over the past decades (Broyer, 2009; Calladine and Bray, 2012;

Fischer et al., 2012; Horch and Birrer, 2011; Müller et al., 2005; Orlowski, 2004). For barn swallows, survival is much lower for juveniles during the post-fledging period than during winter or on migration (Grüebler et al., 2014).

Very high overwinter survival and no significant influence of winter habitat on overwinter survival suggests that winter conditions do not strongly influence whinchat populations, as is also suggested by Hulme and Cresswell (2012). Although conditions during winter and winter habitat degradation have been shown to significantly influence some migrant populations (Baillie and Peach, 1992; Ockendon et al., 2012; Ockendon et al., 2014; Rappole and McDonald, 1994; Sherry and Holmes, 1996; Vickery et al., 2014), as per our findings, some evidence suggests that wintering conditions may not be as limiting as first thought, and that conditions on the breeding grounds or during migration are driving declines (Hulme and Cresswell, 2012; Sherry and Holmes, 1995; Wilson and Cresswell, 2006). An analysis of almost five decades of data for 19 species of Palearctic migrant concluded that climatic conditions on the breeding grounds influence reproductive traits more so than wintering conditions (Ockendon et al., 2013). In line with our findings, barn swallows have higher survival during winter than during the breeding season (Grüebler et al., 2014). Mortality during migration is thought to be especially high for migrants (Newton, 2006b), up to 15 times higher than at any other time for black-throated blue warblers, for example, causing over 85% of the annual mortality for this species (Holmes, 2007; Sillett and Holmes, 2002). Yet for barn swallows, mortality during migration is suggested to be similar to that during winter (Grüebler et al., 2014).

By combining overwinter residency with return rates in the following year, we show that lower residency during winter is not due to winter mortality, but most likely because these individuals have multiple wintering sites, i.e. when a whinchat disappeared from its wintering territory before the end of the winter this was because it had moved to another wintering territory rather than having died. Birds that were resident for shorter periods during winter were just as likely to be seen in the following year as those that were resident for the whole winter, and this was not due to differences in detectability over the winter (see Chapter 3: *Site fidelity*).

Recent studies using geolocators have revealed more than one wintering site for European turtle doves *Streptopelia turtur* (Eraud et al., 2013), great reed warblers *Acrocephalus arundinaceus* (Lemke et al., 2013), thrush nightingales *Luscinia luscinia* (Stach et al., 2012), and veeries *Catharus fuscescens* (Heckscher et al., 2011), although many migrants remain resident at a single site over the entire winter (Bächler et al., 2010; Jahn et al., 2013; Kristensen et al., 2013; Tøttrup et al., 2012). In some cases and as per our results, both single and multiple wintering site strategies have been found across individuals of the same species (Cormier et al., 2013; Delmore et al., 2012).

Another possible explanation for individuals leaving their winter territories is that some whinchats become itinerant and nomadic for some of the winter. Although this behaviour has been suggested for some migrants (Jones, 1995; Moreau, 1972; Salewski et al., 2002b), we believe it is unlikely here because of the strong territoriality exhibited by resident whinchats (see Chapter 3: *Site fidelity*). Movements to additional sites during winter, most likely in response to changing conditions, may be an artefact of extreme conditions one year being reflected in subsequent migrations, as would be expected under the serial residency hypothesis for a species with such high winter site fidelity (Cresswell, 2014). Such 'fixing' of migration phenology may also explain why there was no influence of winter habitat in the previous year on annual survival, even though winter residency differed across sites.

In our study, annual survival did not vary between years, but we lack data to explore yearly differences in overwinter survival over a long time series. There is little doubt that survival estimates are population and species-specific, and that survival may vary between years or between decades, as may the stage in the annual cycle that most influences annual survival. For example, both sand martins and whitethroats *Slyvia communis* have seen huge population crashes in some years due to extensive droughts in the Sahel region of their wintering quarters (Cowley, 1979; Winstanley et al., 1974), and some populations of hirundines have been shown to be limited by rainfall in the Sahel (Robinson et al., 2008). Overwinter survival has been shown to

vary annually for some Neotropical migrants (Dugger et al., 2004). Long-term studies are needed to thoroughly test year effects and the factors responsible. We may also have sampled years where survival was unrepresentative for over-wintering whinchats.

In summary, we present the first estimates of annual and overwinter survival from the wintering ground perspective for whinchats, and some of the first such estimates for any Palearctic migrant. High annual survival, very high overwinter survival, a lack of age or sex differences in survival rates and no influence of winter habitat on annual survival suggests a generalist migratory strategy for whinchats. This study provides strong evidence that conditions on the breeding grounds and during migration influence some migrant populations more than conditions during winter.

CHAPTER 6. LARGE-SCALE MIGRATORY CONNECTIVITY AND VARIATION IN INDIVIDUAL MIGRATORY BEHAVIOUR FOR A DECLINING LONG-DISTANCE MIGRANT

6.1 Abstract

In Europe, long-distance migrants are declining faster than non-migratory species, the causes of which are unclear. Determining the scale of migratory connectivity, how flexible migrants are, and how survival and reproduction are maximised throughout the migratory cycle are essential for understanding these declines and vulnerability to habitat change. Very recent studies have mapped migration from the breeding grounds, but studies from the wintering grounds, which can reveal different information about migration, are scarce. We used miniaturised light-level loggers (geolocators) to describe spatial and temporal aspects of migration, responses to conditions during migration, and variation between both spring and autumn migration and with age and sex for a declining long-distance Palearctic migrant, the whinchat, from a wintering location in West Africa. Migratory connectivity occurred on a large scale, with breeding locations spanning c.1500 km in longitude and c.850 km in latitude across Eastern Europe for the 15 individuals tracked. The timing of migration, routes travelled and the number and location of stopovers varied widely across individuals. Depending on geolocator calibration, whinchats migrated 5947 – 6223 km to the breeding grounds and all birds crossed the Sahara without stopping. Flight speeds over the Sahara were much greater than for other legs of the journey, yet travel speed was not related to wind assistance. Most of the annual cycle was spent wintering and the least amount of time migrating. Spring migration was quicker because birds travelled at a higher velocity, stopped fewer times and flew longer distances between stops, but average stopover duration and the number of days where migratory flight occurred did not differ between spring and autumn. First-winter birds arrived later on the breeding grounds, but other aspects of migration did not differ with age and sex, although sample sizes were low. Migratory connectivity on a large scale and large variation in

migratory behaviour across individuals suggests generalist requirements and perhaps some resilience to drivers of decline at the species level.

6.2 Introduction

In Europe, long-distance migrant birds are declining faster than non-migratory species (Böhning-Gaese and Bauer, 1996; Sanderson et al., 2006; Vickery et al., 2014). The causes and origins of these declines are poorly understood and some declining species show both positive and negative trends over their European breeding range (e.g. see trends in European Bird Census Council, 2012; and in Risely, 2012). Whilst winter habitat degradation is often listed as a cause (Baillie and Peach, 1992; Ockendon et al., 2012; Rappole and McDonald, 1994; Vickery et al., 2014), new evidence suggests that for some species wintering conditions may not be as limiting as first thought (Hulme and Cresswell, 2012; Wilson and Cresswell, 2006). If the sources of decline are not winter habitat quality or availability, then the most likely cause to link migrant declines is the process of migration itself for migrants that are declining faster than non-migratory species.

Determining the specifics of migration is essential for understanding where declines may be occurring and vulnerability to habitat loss and degradation. These are central to the conservation of migrants (Kirby et al., 2008; Woodrey et al., 2005). How specialist or generalist a species is during the non-breeding season, the geographic range of populations, and fundamentally whether migratory connectivity (the extent at which breeding populations also share the same wintering areas, and vice versa) occurs on a small (<100km), medium (<1000km) or large (>1000km) scale determines many aspects of survival and consequently population dynamics (Cresswell, 2014; Webster et al., 2002). How migrants respond to conditions during migration, the influence of geographical barriers on migratory routes and survival, and the number, location and duration of stopovers, can all inform where mortality may be occurring and whether declines may be due to natural or anthropogenic causes. Carry-over effects from one part of the annual cycle to another, the proportion of time allocated to each migratory stage, and age and sex differences in

migratory behaviour can also greatly influence population dynamics (Marra and Holmes, 2001; Newton, 2010a; Sillett and Holmes, 2002). If migrants have the ability to use a wide range of wintering habitats and can respond to changes both within and between years, their flexibility to changing conditions and resilience to habitat loss and degradation will be greater (Cresswell, 2014). Such flexibility may be reflected in the extent of variation in migratory behaviour across individuals.

For many small migratory passerines, the stochastic nature of site selection within the wintering range for juvenile birds undertaking their first migration and the unpredictable nature of the migratory journey itself (Cresswell, 2014; McKinnon et al., 2014) predicts that migratory connectivity will occur only at a large scale (>1,000km, as predicted by the serial residency hypothesis (Cresswell, 2014)). This is because juvenile birds have no prior knowledge of migratory routes or destinations. This, coupled with the strategy of high wintering site fidelity in subsequent years (Cresswell, 2014; see Chapter 3: Site fidelity; Holmes and Sherry, 1992; Holmes et al., 1989; Kelsey, 1989; Marra, 2000; Salewski et al., 2000; Sauvage et al., 1998; Skilleter, 1995), also predicts that migrants will have generalist requirements outside of the breeding season in response to unpredictable conditions (Cresswell, 2014).

Conditions experienced during migration itself often influence population dynamics, and how migrants respond to these conditions is often reflected in their migratory behaviour (Newton, 2010b). Migrants often adjust their migration speed, travel routes, and the location and duration of stopovers in response to both weather conditions and the position and width of ecological barriers (Åkesson and Hedenström, 2007; Alerstam and Lindström, 1990; Biebach et al., 1986; Klaassen et al., 2008; Liechti, 2006). Wind and weather affect flight paths, flight speed and the timing of migration (Åkesson and Hedenström, 2007; Calvert et al., 2009; Richardson, 1990; Schaub et al., 2004), along with survival en route (Newton, 2006b, 2007). Large ecological barriers such as deserts may demand long non-stop flights and high fat stores (Chernetsov, 2012b). Stopover decisions must allow sufficient energy reserves to be accumulated or replenished before and after migratory flight and non-stop barrier crossings; yet the more stopovers relied upon and the greater

the dependency upon specific locations (i.e. low flexibility to use alternative sites), the higher the risks and implications of losing one or more stopover locations to habitat loss (Newton, 2004). Decisions of where to stop and refuel and how long to remain at stopovers can therefore be key to the success of migration and consequently survival (Eraud et al., 2013); however species are highly diverse in their migratory strategies and the amount of fuel reserves they carry (e.g. Jenni-Eiermann et al., 2010). Migrants therefore often travel faster over barriers (Alerstam, 1993; Fox et al., 2003), and migrate along routes that avoid them (Alerstam, 2001). Stopovers are often situated immediately before or after barriers and are longer in duration if so (Chernetsov, 2012b), and migrants have more extensive pre-migratory fattening before crossing larger barriers (Rubolini et al., 2002). Conditions during migration consequently influence both temporal and spatial aspects of migration, and it is important to identify these key aspects, particularly if we aim for site-based conservation. This is especially true since the implications of conditions experienced during migration may increase if migratory behaviour varies little across the species as a whole.

Events and conditions experienced in one part of the annual cycle carry over to influence others (Marra et al., 1998; Sillett et al., 2000; Webster et al., 2002). The influence of wind and weather on migration can impact future survival, breeding and productivity, for example (Drake et al., 2014). Because each aspect of the migratory cycle is far from distinct, how migrants partition this annual cycle between stages also has consequences for survival and future reproduction. Survival is often highest during the winter (see Chapter 5: Survival, and Holmes et al., 1989), and lowest during migration (Sillett and Holmes, 2002), which may explain why many migrants spend most time on the wintering grounds (Webster et al., 2005). Spring migration is often more rapid because the disadvantages of arriving late on the breeding grounds are greater (Newton, 2010a; Nilsson et al., 2013; Tøttrup et al., 2012; Tryjanowski and Yosef, 2002), and so stopovers are often longer and more frequent during autumn migration (Dingle, 1996; Newton, 2010a).

For many species, migratory phenology differs between demographic groups. Younger birds often migrate slower and arrive later on the breeding grounds than adults, which is often suggested to be a result of their inexperience (McKinnon et al., 2014; Newton, 2010a). Males often migrate ahead of females (Dierschke et al., 2005; Francis and Cooke, 1986; Otahal, 1995; Yunick, 1988) and are the first to arrive on the breeding grounds (Francis and Cooke, 1986; Newton, 2010a; Smith et al., 2009). Older males often arrive before first year males (Enstrom, 1992; Francis and Cooke, 1986; Smith et al., 2009). For males, early arrival is frequently linked to greater reproductive success because it allows greater territory and mate choice, a higher likelihood of mating, and earlier breeding, and consequently a longer breeding season and a greater opportunity of repeat nesting (Aebischer et al., 1996; Amrhein et al., 2007; Bensch and Hasselquist, 1991; Brooke, 1979; Currie et al., 2000; Lozano et al., 1996; Potti and Montalvo, 1991; Smith and Moore, 2005; Wiggins et al., 1994b). Females that arrive earlier also benefit from earlier breeding and recruit more offspring (Smith and Moore, 2005). Such benefits may vary across individuals (Forstmeier, 2002), are often greater for males, and arriving too early can even be detrimental for some species (Møller, 1994). Any differences in migratory phenology between demographic groups is often greater during spring migration because of greater time constraints (Newton, 2010a). Differential survival or lower reproductive success occurring for a particular demographic group due to differential migration can lead to skewed population dynamics and population declines (Steifetten and Dale, 2006), and so knowledge of whether migration phenology differs between adults and juveniles or between males and females can give insights as to whether a particular demographic group may be more susceptible to any particular driver of decline.

The accurate tracking of individuals and their behaviour during migration is key to obtaining information regarding factors affecting migration. A growing number of very recent studies have employed miniaturised light-level loggers (geolocators) to track the migratory routes of small passerines from the breeding grounds, yielding much important information (see Bridge et al., 2013 and references therein), yet fundamental details are still lacking (Eraud et al., 2013), especially from the

wintering perspective. If migratory connectivity occurs only on a large scale as is predicted for passerine migrants (Cresswell, 2014), then the details of migration gained from geolocators will change depending on whether migration is tracked from the breeding or wintering grounds. For example, we can explore the scale at which European populations are influenced by habitat degradation in a small region on the wintering grounds. Furthermore, because the accuracy of locations determined from geolocators reduces closer to the equator, geolocators deployed on the wintering grounds may provide more reliable year-round results. A recent study found the inaccuracy of locations was reduced by half when mapping locations from the wintering grounds (McKinnon et al., 2013b). Consequently, there is a growing need to study migration from the wintering perspective.

We use data from geolocators fitted to a single wintering population of whinchats to describe both spatial and temporal aspects of the migratory cycle, how these relate to the theory of migrants as generalists, and the implications for the conservation of declining long-distance Palearctic migrants. We explore and evaluate:

1. The degree of migratory connectivity and evidence of a generalist migratory strategy. We predict:
    - Large-scale connectivity (i.e. >1000km spread across breeding locations) because of the stochastic nature of first year site selection within the wintering range and lower site fidelity on the breeding grounds for whinchats (see Chapter 3: *Site fidelity*).
    - Wide variation in aspects of migratory behaviour across individuals.

2. How individuals respond to conditions during migration, by investigating:
    - The influence of ecological barriers and wind conditions on travel speeds and stopover locations. We predict faster travel speeds over ecological barriers, and stopovers directly after them.
    - Whether arrival and departure times are related. We predict that where there is no relationship, conditions during migration are likely to influence migration speed.

3. How individuals allocate time throughout the annual cycle and differences between spring and autumn. We predict:
   - The most time will be spent wintering and the least time migrating
   - Faster spring migration due to fewer stopovers.
   - Less variation in aspects of migration between individuals in spring.

4. Age and sex differences in migratory behaviour. We predict:
   - Male and adult birds will be the first to depart from the wintering grounds and arrive at the breeding grounds.
   - Any age differences will only occur during spring, because all birds have experienced one complete annual cycle upon reaching the breeding grounds.

6.3 Methods

See Chapter 2: *General methodology* for details for study sites and capturing individuals. All mean values presented in Methods and Results are ± one standard error.

Geolocator deployment

We used miniaturised archival light-level loggers (referred to as geolocators or loggers) to describe the spatial and temporal aspects of migration. We used model MK6740 developed by the British Antarctic Survey (BAS), with 10 mm light stalks positioned at a fixed angle of 45°, and with the tube for harness attachment placed on the back instead of the end of the logger. Geolocators provide locations accurate to approximately 200 km (Fox, 2010; Fraser et al., 2013; Lemke et al., 2013), which was sufficient to address the aims of this study. We deployed 49 geolocators between 12th February and 8th March 2013 across three study sites (site A = 11, site H = 24, site J = 14; see Chapter 2: *General methodology* for details of study area and sites). 29 birds were aged as first-winter, 15 adult, and 5 of unknown age, of which

31 were male, 14 female, and four of unknown sex. Birds were captured with mist nets and audio playback of whinchat calls and song and loggers were fitted with a leg-loop backpack system (Rappole and Tipton, 1991) using 0.8mm diameter clear elastic beading thread. This attachment method is considered to be favourable compared to alternative methods (Costantini and Møller, 2013). We made a large number of harness sizes for each field session so that modifications were not necessary during fitting. Average geolocator mass plus harness at deployment was 0.74 ±0.02 g, equal to 4.8% of the average body weight (15.6 ±0.05 g; range = 4.3 – 5.3%). Loggers were fitted to birds with a wing length ≥ 77 mm (flattened wing chord: average across birds fitted with loggers = 77.4 ±0.2, range = 77 - 81 mm). Birds with pectoral muscle scores of 0 were excluded regardless of wing length (fat scores were not used because these were minimal across all wintering birds captured as part of a larger study). Birds were ringed with unique combinations of two or three colours, including a striped ring for birds with geolocators and an aluminium ring for birds with no geolocator. Birds were released at the location at which they were captured.

Resighting individuals and retrieving geolocators

To determine whether individuals were resident, resighting efforts for birds with geolocators were carried out from their capture until May 2013 when most individuals were assumed to have departed (see Chapter 2: *General methodology* for resighting protocol). 44 of 49 birds were resighted at least once after capture (on average up to 26 ±2.8 days after capture, range = 3 – 63 days). The last individual with a geolocator was seen on 20th April 2013. Resighting efforts for returning birds began in October 2013 and continued until we were confident that we had detected all returning birds (individuals return to the same territory used in the previous year – see Chapter 3: *Site fidelity*). We retrieved 15 geolocators by capturing returning birds with spring traps and playback (spring traps allowed us to easily target specific individuals). A 16th individual was found in the following winter after analyses had been performed, and so is not included in the following results. Because we fitted geolocators late in the wintering season when possible transients may be moving

though the study site (suggested by increased sightings of unringed whinchats during this time), we may have fitted geolocators to transients. This perhaps explains lower return rates than previously observed for birds without geolocators (return rate across birds without geolocators across a 3-year study = 54% (see Chapter 5: *Survival*), birds with geolocators = 31%. For example, five individuals were never seen after capture, one of which was resighted and captured late in the following year (March 2014). One individual resighted after capture was only resighted again in March 2014. The effects of fitting geolocators, including those of different geolocator and harness design, are thus being explored in a larger, longer-term study.

Light data analyses

Of the 15 loggers retrieved, 10 provided traces of the entire migratory cycle and five were incomplete (one battery failed on the breeding grounds and four during spring migration). Raw data were downloaded, viewed and preliminarily edited using the BASTrack software suite (British Antarctic Survey, Cambridge, UK; see Fox, 2010 for an overview of the following processes). Because the clocks within loggers may gain or lose small amounts of time when recording, we adjusted for clock drift, assuming that any drift was linear. We used the Transedit2 software to view raw data as light curves over time. Loggers record light on an arbitrary scale of 0 – 64, from which a 'threshold' value is chosen to define sunrise and sunset times (henceforth 'twilight events'): a sunrise was defined when light levels exceed this threshold, and a sunset was defined when light levels dropped below this threshold. We used a threshold value of 2, which is close to civil twilight. False twilight events due to shading from weather or vegetation were identified and removed with the 'minimum dark period' filter, which removes any sunrise and sunset events occurring within a defined number of hours (4 in this analysis) of a true sunrise and sunset (for a review and exploration of the effects of enviromental factors on geolocator data, see Lisovski et al., 2012b). Data were then visually inspected to ensure that only one sunrise and sunset occurred within any 24-hour period, after which we used the LoessFilter in the R package 'GeoLight' (Lisovski et al., 2012a; Lisovski and Hahn, 2012) to validate

twilight events and identify those influenced by shading events at dawn and dusk: a polynomial regression of twilight events identified residuals that were greater than three times the interquartile range and are therefore likely to be erroneous (Lisovski and Hahn, 2012). We checked outliers within the original data before removing them (because large movements resulting from migration were sometimes incorrectly identified as outliers) (mean = 4 ±0.6% of total twilight events were removed for each logger).

To obtain latitude from twilight events derived from a given light threshold value, a corresponding 'sun elevation angle' is required. If local weather conditions differ between staging locations, the corresponding sun elevation angle will differ also. Consequently, there is likely to be a different sun elevation angle for wintering and breeding locations (henceforth 'winter' and 'summer'). To determine the correct sun elevation angle for winter (SEA_W) and summer (SEA_S), we carried out two calibrations. For SEA_W we used the LocatorAid software from the BASTrack software suite, which uses known residency times and wintering location to calculate the corresponding wintering ground SEA. This averaged -4.8 ±0.07 across 14 individuals with known residency times. We used this mean value for one bird with an unknown residency time. To determine SEA_S we used the Hill-Ekstrom calibration method (Ekstrom, 2004; Hill and Braun, 2001; see Tøttrup et al., 2012) for a period of two months when birds were assumed to be stationary, starting five days from arrival at the breeding grounds. We calculated the variance in latitude generated from a SEA of -1 to -6 at -0.5 increments, and chose the value that generated the least variation in latitude. SEA_S ranged from -2.0 to -4.5 (mean -3.5 ±0.4) across the 15 loggers. In seven of 15 cases an obvious minimum variance was not found or an unrealistic sun elevation angle inferred (< -2.0), most likely because this method is used chiefly for calibration during the equinox when latitude cannot be determined, and not for times outside of this period. Here we used the mean SEA_S as determined from loggers where calibration was possible (-3.5).

Once a corresponding SEA_W and SEA_S were known for each logger, noon and midnight locations were derived from sunrise and sunset times using the 'coord'

function in the Geolight package (Lisovski et al., 2012a; Lisovski and Hahn, 2012), where latitude is calculated from the length of the solar day and night, and longitude from local solar noon and midnight. We derived latitude for both SEA_W and SEA_S for all locations, except for wintering locations and any stopovers close in space and time to the wintering period (i.e. before crossing the Sahara during spring migration) because SEA_W was known during this time. Latitude data ±15 days of the vernal and autumnal equinoxes (20th March and 22nd September) are inaccurate because day length (daylight hours) does not vary substantially, and so were excluded from all analyses. Latitudes ±16-20 days from the equinoxes were used conservatively by visually comparing with previous and future locations and any subjective locations removed.

Because whinchats are nocturnal migrants (Berthold, 2001; Fusani et al., 2009) we used midnight locations only for all analyses and when plotting locations, apart from for verifying short stopovers of c. two days, where we used noon locations also. Stopovers were defined by birds being stationary for at least two days, indicated when latitude and longitude did not vary more than c.100 km for at least two midnight locations and three noon locations. Because our data were relatively clean (i.e. little abnormal shading at dawn and dusk), stopover locations were well defined, and so we were confident in our ability to identify short stopovers. To account for the inherent inaccuracy of fixes derived from geolocators, we used 2-day averages of locations derived using SEA_W and SEA_S when plotting migratory routes. Stationary periods were plotted as the mean location of all fixes during these times. For all maps, we show the average of the locations derived from both SEA_W and SEA_S and show the respective differences in latitude derived using these different sun elevation angles as error bars where displayed (see figure-specific legends for details). Note that SEA_S was not determined for one individual that was not stationary during the breeding season (see *results* for details). Locations were mapped in ArcGIS version 10.1 (ERSI, 2012). We used Microsoft Excel version 14.4.4 (2011) to overlay migratory routes with spatial maps. We calculated minimum great-circle distances between consecutive stopovers and wintering/breeding locations (i.e. distances accounting for the curvature of the Earth) using the measure tool in

ArcGIS. Where we were confident that a non-direct route was followed between staging areas, we calculated the minimum distance travelled along that route. When calculating flight speeds of birds, because we could not determine any stopovers less than two days in length, we present minimum flight speeds in a 24 hour period, calculated by dividing the distance travelled each day and dividing this by 24, the number of hours in a day.

Wind assistance analyses

We used data on wind assistance (the extent to which wind conditions aid or hinder flight, referred to also as wind profit) to explore the influence of wind speed and direction on a bird's ground speed. We obtained surface wind data from the National Centre for Environmental Prediction (NCEP)/National Centre for Atmospheric Research (NCAR) Reanalysis dataset (Kalnay et al., 1996) at a resolution of 2.5 degrees of latitude and longitude. Data were given as the U and V components of wind (which describe the east-west and north-south components of wind, respectively), from which we derived wind speed and direction. Wind data at midnight were matched with each midnight location during migratory flight, plus the last and first day at the departure and arrival locations, respectively. For stationary departure and arrival locations we used the mean location, and averaged between winter and summer sun angle locations for locations when migratory flight was occurring. For each location we calculated wind assistance (*WA*) in metres per second (m/s) with the following equation, as per Kemp 2013:

$$WA = \mathrm{Wspd} * \cos\alpha + \sqrt{z^2 + (\mathrm{Wspd} * \sin\alpha)^2} - z$$

Where wind assistance is a function of wind speed (Wspd), the bird's airspeed (*z*), and the angular difference between the direction the bird is flying and the direction the wind is blowing towards (α). The equation assumes that birds have a fixed airspeed and adjust their heading in response to side-winds (Kemp et al., 2012).

We averaged values for wind assistance between all locations along each flight leg (i.e. between consecutive stationary periods) and determined whether a flight was over the Sahara, the main ecological barrier along the migratory route.

Statistical analyses

Statistical analyses were carried out in R version 3.0.1 (R Development Core Team, 2013) and RStudio Version 0.98.507. We used General Linear Models to test both a) the relationship between arrival time at the breeding grounds and the last day at the winter territory or at a stopover south of the Sahara, and the relationship between arrival time at the wintering grounds and b) the number of days and the last day on the breeding territory. To explore the influence of wind assistance and ecological barriers on travel speed, i.e. ground speed, we fitted a Mixed Effects General Linear Model of ground speed ~ wind assistance + flight type (barrier or non-barrier crossing), controlling for individual as a random effect (as we had multiple data for each bird) and the number of locations included in each flight leg (because the probability of a short (i.e. undetectable) stop may increase with the number of fixes) using the nlme package (Bliese, 2013). We used paired *t*-tests and paired Wilcoxon tests to compare aspects of migration between spring and autumn, and *t*-tests and Wilcoxon tests to compare migratory behaviour between first-winter and adult birds, and males and females. The sequential Bonferroni procedure (Rice, 1989) was used to correct for Type 1 error rate. Migration speeds could not be compared between sexes in autumn due to uncertainty around the equinox, and the duration of time spent on the breeding grounds and departure times of males and females could not be compared due to low sample sizes. A statistical significance level of $p < 0.05$ was chosen to reject null hypotheses.

6.4 Results

1. Connectivity and individual variation

Migratory connectivity occurred over a large scale (Figures 6.1 and 6.2) with a breeding ground span of 1445 to 1526 km (longitudes 20.62 E and 44.37 E) from our single wintering population (depending on whether locations were derived from summer (SEA_S) or winter sun elevation angles (SEA_W), respectively). When including summering locations of the individual that was not stationary during the breeding season (see Figure 6.3 map marked with a triangle), the breeding span increased to 1723 or 1750 km (16.91 E to 44.37 E). Breeding locations were closer in latitude than longitude, spanning 840 km (54.89 N to 60.59 N) if locations were derived from SEA_S, and 890 km (51.16 N to 59.48 N) if derived from SEA_W (Figure 6.4). The maximum possible north to south summer range of the wintering population when including all locations derived from both summer and winter sun elevation angles was 1050 km. Individuals were sedentary for the breeding season until commencing autumn migration, with the exception of one individual that moved gradually east for 61 days before moving to a location >1000km west for a further 54 days with a gradual southward movement before autumn migration, perhaps suggesting that this individual failed to breed (Figure 6.3, map marked with a triangle). Despite limited complete routes for autumn migration, results suggest a loop migration (Figures 6.1 and 6.2).

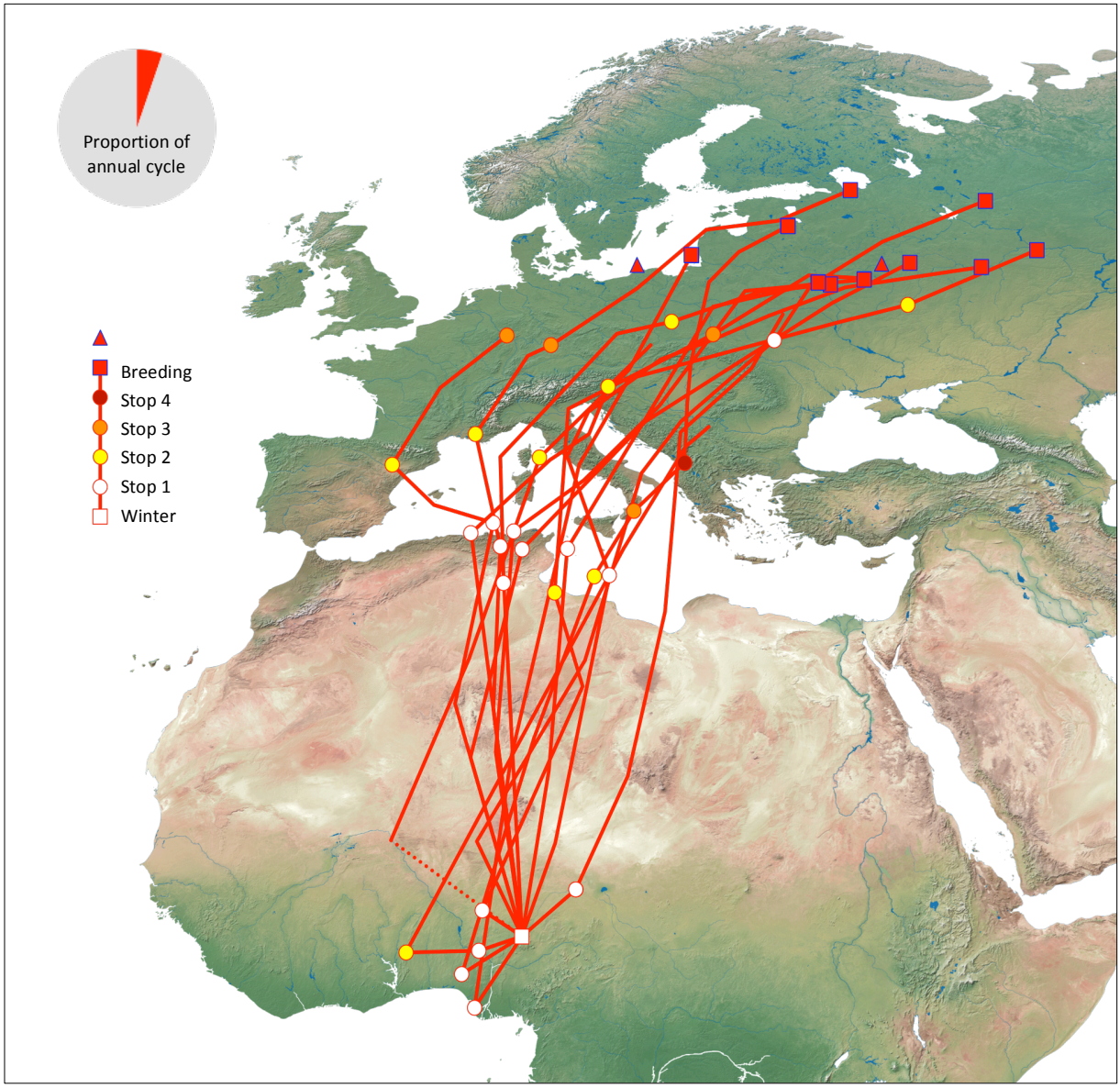


Figure 6.1. Spring migration routes including stopovers (circles) of 15 whinchats from their winter territories (white square) derived from 2-day averages, plus breeding ground locations for 11 whinchats (red squares; four loggers failed en route). One bird changed locations during the breeding season (red triangles; see individual map marked △ for details). Stopovers are coloured in sequence for each bird: white = first, yellow = second, orange = third, dark red = forth. Dotted lines represent uncertainty in routes around the equinox. The red section of the grey circle (upper left) represents the proportion of the annual cycle spent on spring migration.

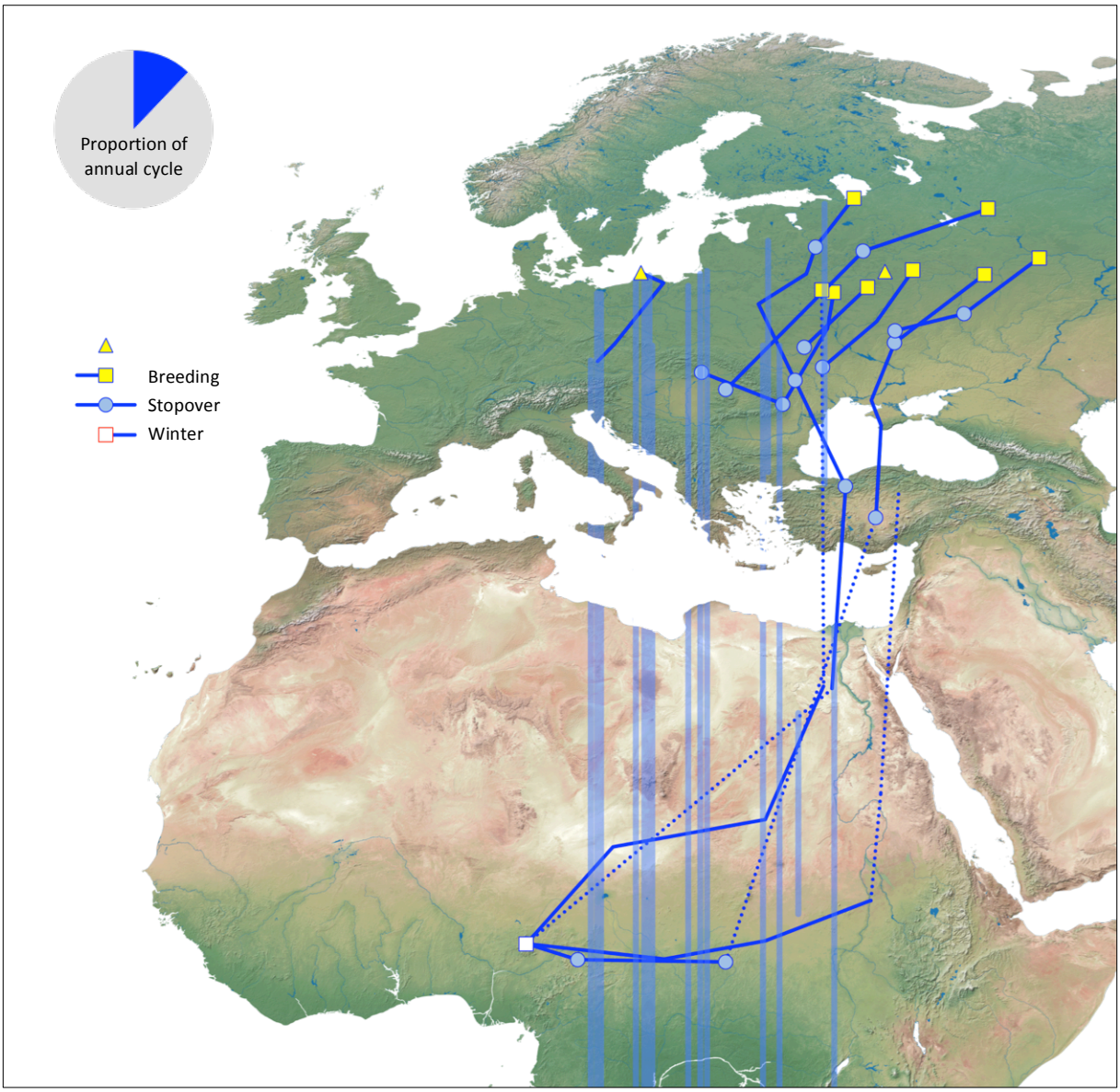
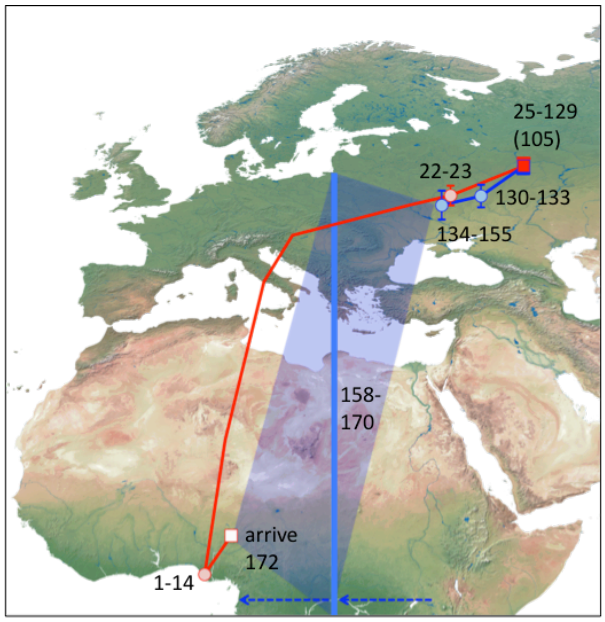


Figure 6.2. Autumn migration routes derived from 2-day averages including stopovers (light blue circles) of 10 whinchats from breeding territories (yellow squares) to the winter territory (white square). One bird changed locations during the breeding season (yellow triangles; see individual map marked △ Figure 6.3). Dotted lines represent uncertainty in routes around the equinox. Light blue vertical lines show possible locations of stopovers during the equinox when latitude cannot be determined. The blue section of the grey circle (upper left) represents the proportion of the annual cycle spent on autumn migration.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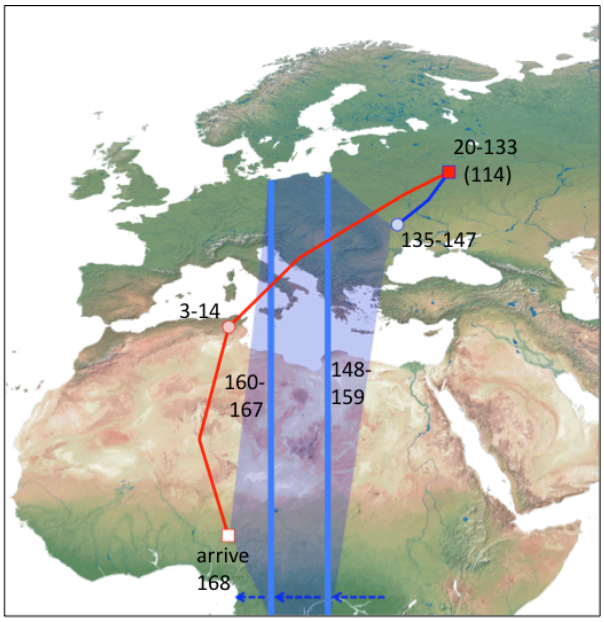
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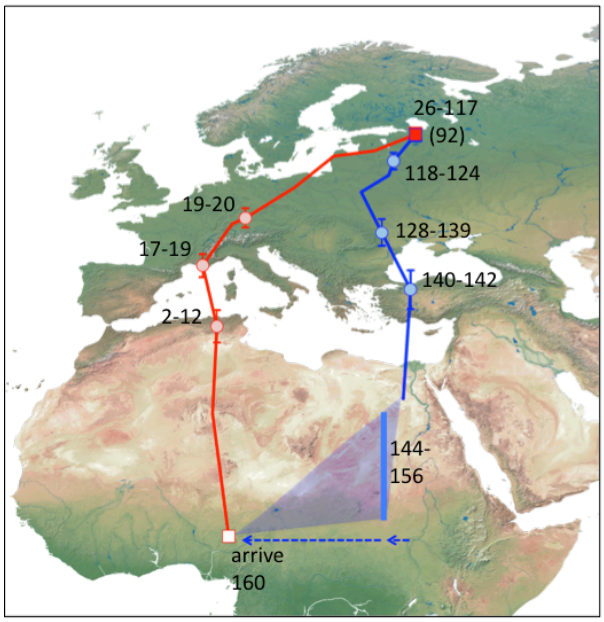
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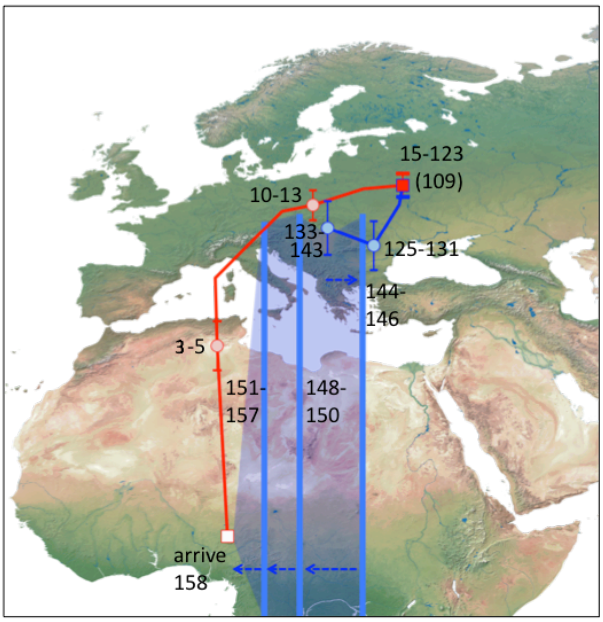
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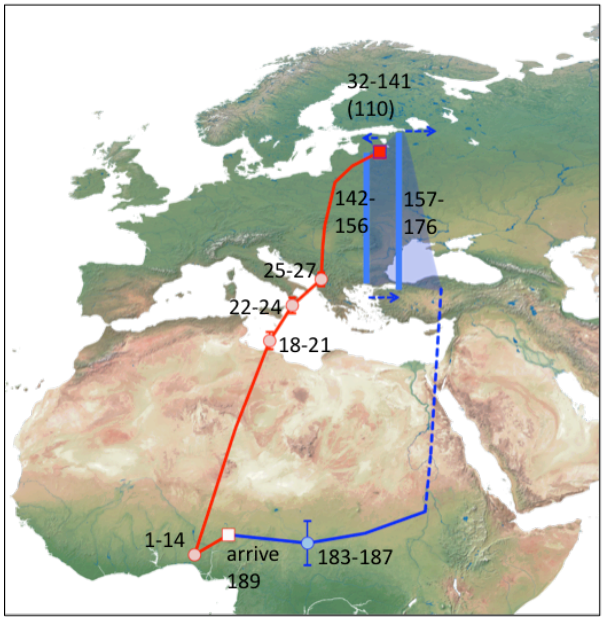
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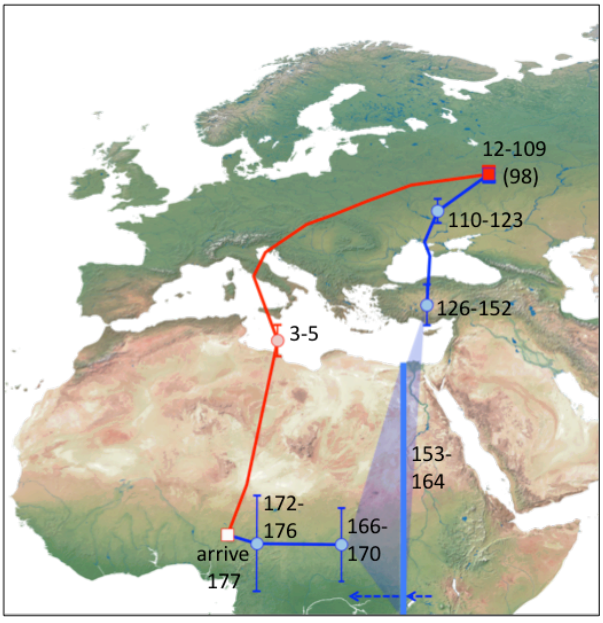
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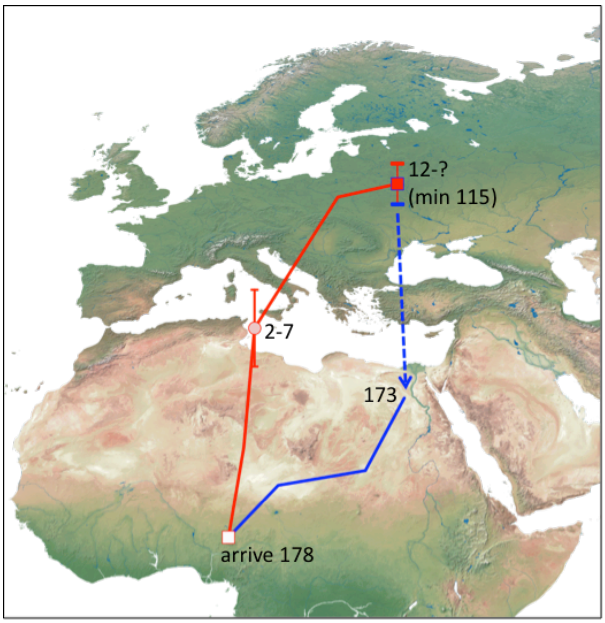
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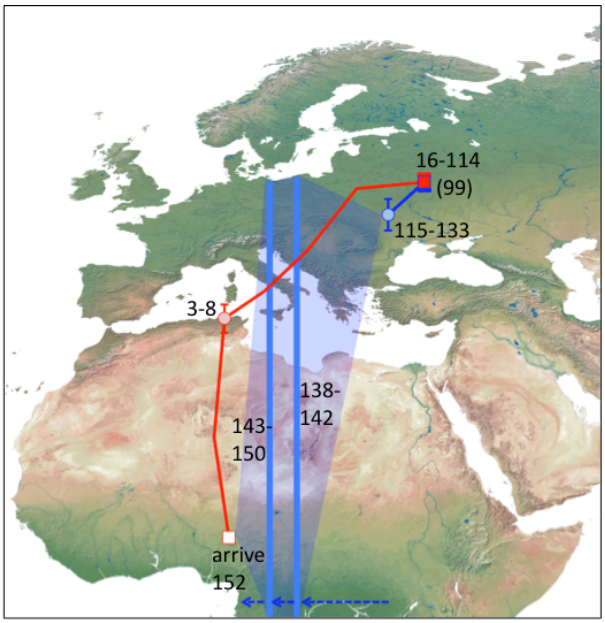
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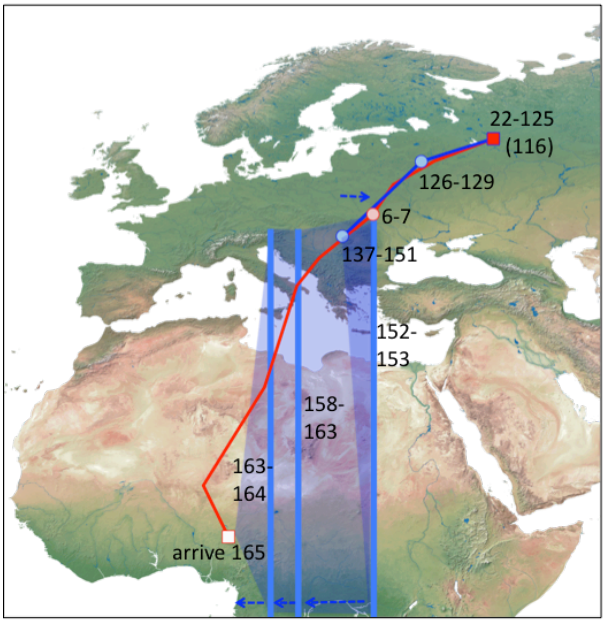
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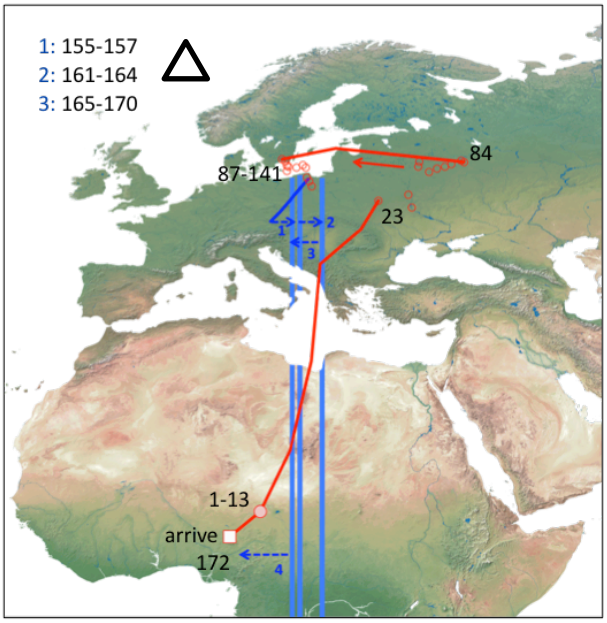
164
arrive 165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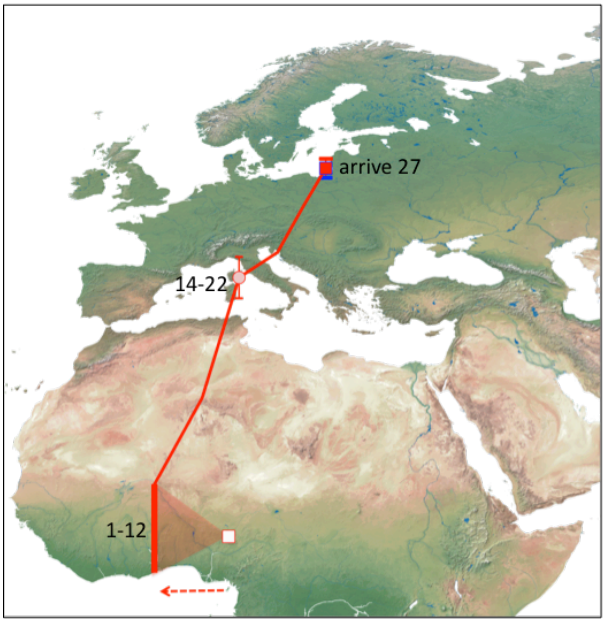
172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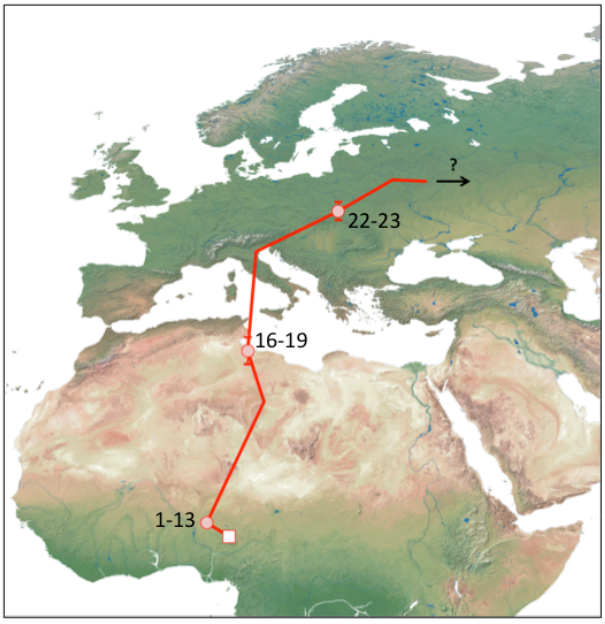
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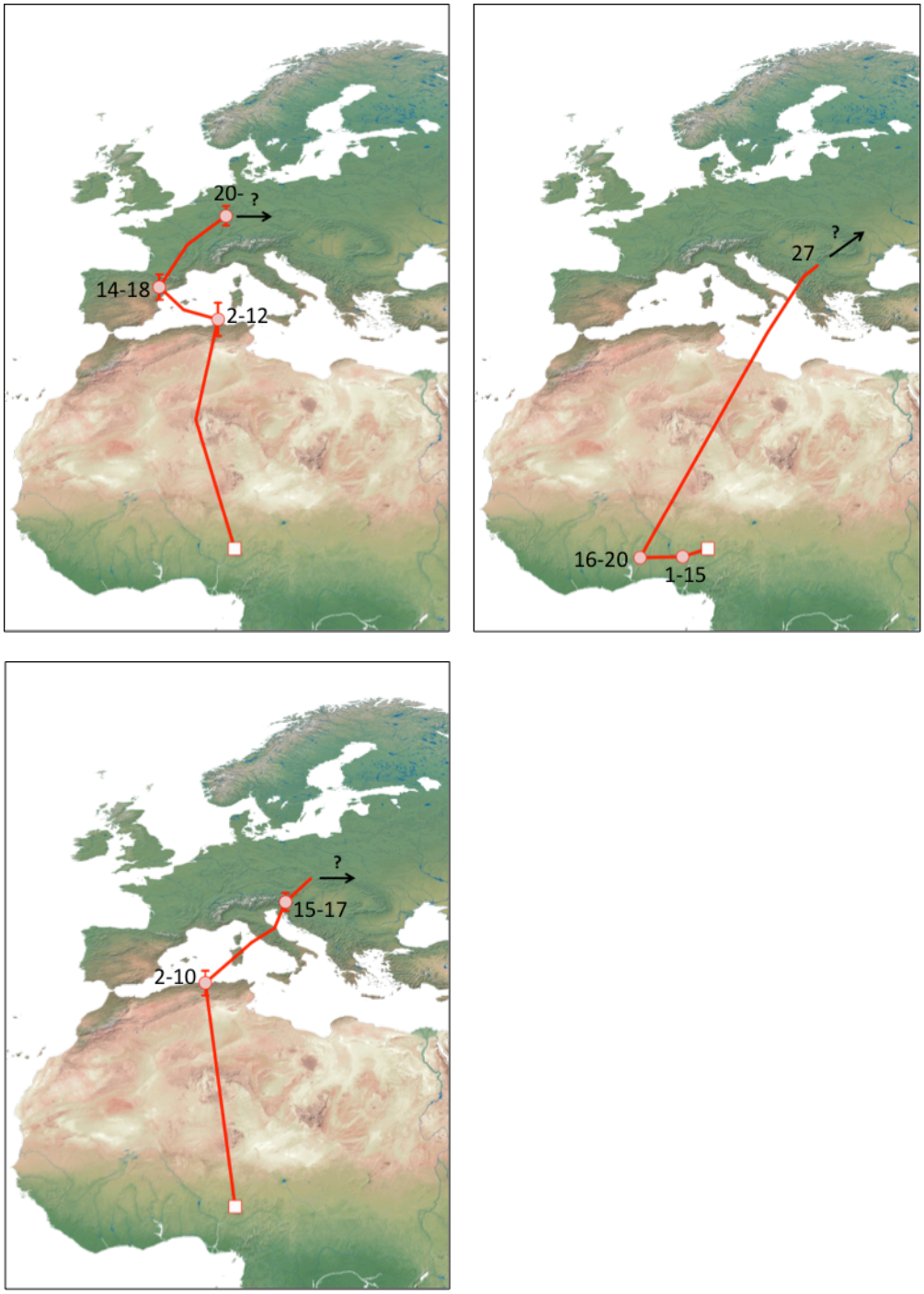

Figure 6.3. Migration maps of the annual cycle of 15 individuals showing spring migration (red line) to the breeding grounds (red square) and autumn migration (blue line) back to the winter territory (white square). Migratory routes are presented as two-day averages (the average location across each two consecutive days). Timings of stopovers during spring (light red circles) and autumn migration (light blue circles), and arrival and departure from breeding grounds are shown as number of days since departure from the winter territory. The number of days spent on the breeding grounds

is shown in brackets. For all traces where the sun elevation angle differed between the winter and summer grounds (resulting in a variation in latitude - see methods), the mean latitude is used, except for those south of the Sahara during spring migration because these were close in both time and space to the wintering grounds. Error bars show the winter (upper) and summer (lower) latitude for any stationary periods where mean latitude is plotted – note that these reverse for locations south of the Sahara. Latitude could not be determined 15 days either side of the equinoxes – stopovers during these are represented by vertical red and blue lines for spring and autumn, respectively, with approximate flight paths shown with shaded areas. Dashed arrows show the direction of movement between these stops. Any latitudes ± 16-20 from the equinoxes were used along with knowledge of locations before and after these periods to refine stopover locations where possible, given the assumption that migration occurs in a northerly or southerly direction during spring and autumn migration, respectively. Flight paths during these periods are also less accurate and are represented with dashed connecting lines. Note that five loggers gave incomplete traces. The map marked △ shows the trace for one individual that moved locations during the breeding season: only the winter sun elevation angle was used to determine locations for this individual because the lack of stationary periods prevented calibration during the breeding season.

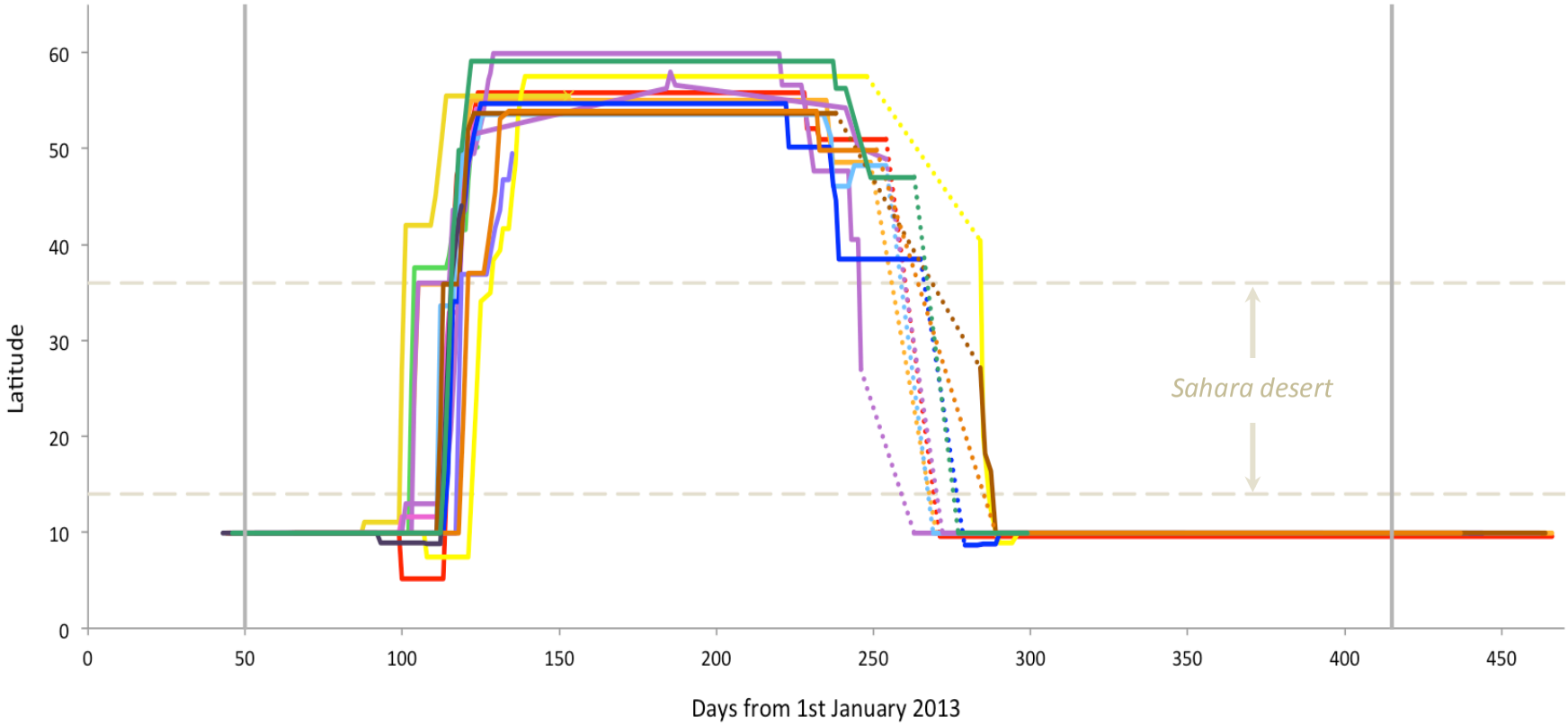

Figure 6.4. Location determined by latitude throughout the annual cycle (days from 01st January). Grey lines represent the start (left) and end (right) of one year, as defined from approximate capture date for birds fitted with geolocators. Each colour represents one individual – note that five of 15 geolocators have incomplete traces due to failure either on (*n* = 1 logger) or before (*n* = 4 loggers) reaching breeding grounds. Dotted lines show uncertainty in latitude due to the equinox. Horizontal dashed lines represent the north and south bounds of the Sahara desert.

Migratory behaviour varied across individuals, with variation in the timing of migration, routes travelled during both spring and autumn migration, and the location of stopovers (Figures 6.1 and 6.2; Figure 6.3 shows individual routes and timings. *See supplementary Appendix Table A.1 for means and variation across individuals plus sample sizes for the following results*). The average minimum distance travelled from the primary winter territory to the breeding grounds was 5947 km (±204.7, SEA_W) to 6223 km (±190.0, SEA_S), depending on the sun elevation angle used to determine breeding locations (summer range 5026 – 7516 km SEA_W, 5597 – 7676 km SEA_S; see *methods*). Birds stopped between four and seven times during migration (spring and autumn migration combined; mean = 6 ±0.4). On average, birds departed winter territories or the surrounding area between 28th March and 28th April (average 15th April, ±2.3 days). The last day south of the Sahara before migrating was between 9th April and 1st May (average 20th April ±1.6 days). Average arrival date at the breeding grounds was 5th May (±2.0 days; range 24th April to 19th May).

Birds remained on the breeding grounds for 105 days on average (±3.0, range 92 – 116 days). Arrival time on the breeding grounds was not related to the last day on the winter territory (β = 0.17, $t_{2,8}$ = 0.7, SE = 0.24, p = 0.51), or the last day at a stop south of the Sahara (β = 0.57, $t_{2,8}$ = 1.9, SE = 0.31 p = 0.10; overall model: $F_{2,8}$ = 4.7, R^2 = 0.54, p = 0.045, n = 15). Autumn migration commenced between 8th August and 5th September (mean 10th August ± 3.1 days), with birds arriving back on the wintering grounds between 20th September and 23rd October (mean 4th October ± 3.1 days). Arrival on the wintering grounds did not depend upon the number of days spent at the breeding grounds (β = -0.46, $t_{2,8}$ = -0.6, SE = 0.79, p = 0.59) or day of departure from the breeding grounds (β = 0.92, $t_{2,8}$ = 1.2, SE = 0.75 p = 0.27; overall model: $F_{2,5}$ = 0.9, R^2 = 0.26, p = 0.46). Some aspects of migration, specifically the location of stopovers immediately after the Sahara crossing and the northerly route over the Sahara were less variable across individuals (Figure 6.1).

2. Conditions during migration

All birds travelled directly over the Sahara without stopovers (defined by a stationary period of at least 2 days in this study; see Methods) and travelled significantly faster when doing so (linear mixed-effects model (LMM) with individual as a random effect and with two location fixes: *barrier crossing*: predicted minimum flight speed = 45.9 km/hr, t = 12.6, SE = 5.1, $p < 0.0001$, *non-barrier crossing*: predicted minimum flight speed = 21.5 km/hr, t = -8.2, SE = 4.3, $p < 0.0001$; df = 24, n = 53 observations for 15 individuals. Observed minimum flight speeds: *barrier crossing* = 46.4 km/hr ±3.6, range = 32 – 64, *non-barrier crossing* = 20.1 km/hr ±1.4, range = 12.0 – 42.0, all speeds averaged between summer and winter sun elevation angle locations, Figures 6.4 and 6.5). Minimum ground speed was not related to wind assistance (LMM: ground speed ~ wind assistance + flight type (barrier/non-barrier), with individual as a random effect and two location fixes: *barrier crossing* predicted minimum flight speed = 46.3 km/hr, *non-barrier crossing* predicted minimum flight speed = 22.1 km/hr, df = 35, SE = 0.22, p = 0.74, n = 53 observations for 15 individuals). 11 birds (73%) stopped immediately after crossing the Sahara (i.e. within ~500 km of the north coast of Africa; Figure 6.1). After leaving their winter territory, six birds (40%) stopped once and one bird (7%) stopped twice before crossing the Sahara.

3. Time allocation and spring and autumn differences

More than half (53.7% ±0.94) of the annual cycle was spent on the wintering grounds and the smallest part of the annual cycle was spent migrating (5.4% ±1.2) (Figure 6.6). Total migration time including stopovers was significantly shorter in spring (mean difference = 24 ±4.9 days; Table 6.1). In spring, birds travelled faster (average minimum flight speeds, averaged between summer and winter sun elevation angle locations: *spring* = 28.6 ±1.8 km/hr, *autumn* = 20.5 ±2.2 km/hr, mean difference = 6.5 ±1.8 km/hr), stopped fewer times (*spring*: range = 1-4 stops, average = 2 ±0.3, Figure 6.1; *autumn*: range = 3-5 stops, average 4 ±0.3; Figure 6.2; average difference between spring and autumn = 2 ±0.4), and consequently spent on average 23 ±5.3 fewer days at stopovers. There was no difference in the mean duration of

stopovers or the number of days on which migratory flight occurred between spring and autumn migration (mean difference = 2.5 ±1.0 days). Because fewer stopovers were made during spring, most individuals (86%) travelled for longer between stopovers in spring (mean difference = 2.0 ± 0.42 days between stops) and travelled faster between stopovers (average 5.3 to 8.1 km/hr (±1.8 – 1.7 km/hr) faster; Table 6.1).

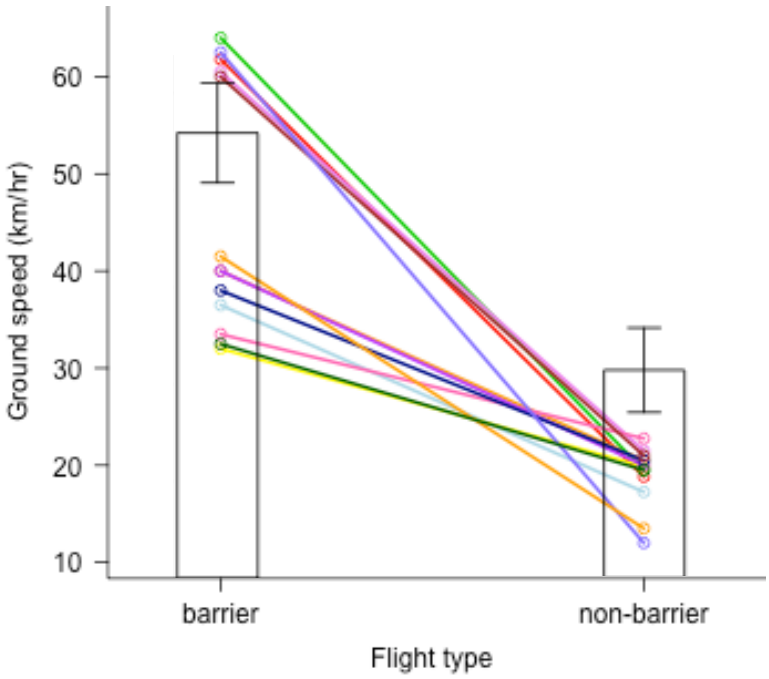

Figure 6.5. Comparison of ground speed (km/hr) during spring migration over the main barrier, the Sahara desert, and at other times during migration, e.g. over Europe, where large ecological barriers were largely absent. Bars show the mean predicted value for ground speed predicted from the mixed model presented in the results. Where multiple flights were made between stopovers for non-barrier flights, the mean speed for that flight type is presented. Speeds for barrier crossings are from one single value for each bird because in all cases no stops were made during a barrier crossing. Each line is one individual, the colour of which matches that used for the migratory trace of latitude in Figure 6.4; *n* = 13 due to limited data for two loggers.

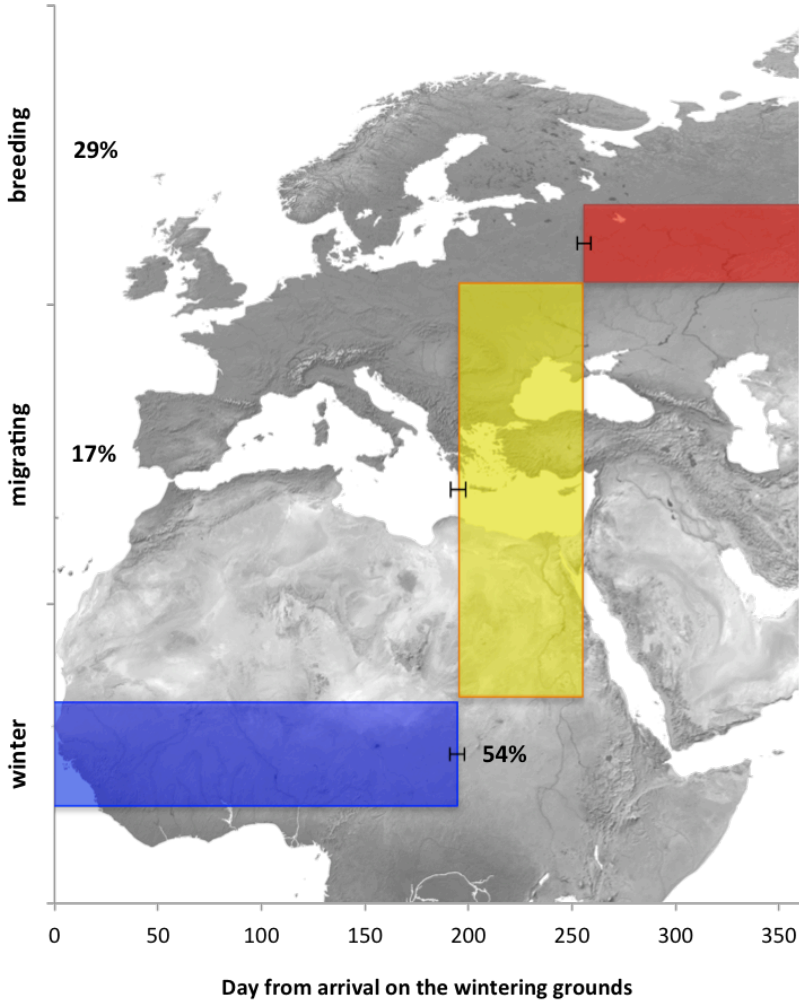

Figure 6.6. The annual cycle for whinchats, showing the amount of time allocated to the three main aspects of the annual migratory cycle (wintering = blue, migration = yellow, breeding = red), shown as both the number of days from the start of the wintering period (x axis) and the percentage of the annual cycle (% value). Values are means ± one SE from the migratory traces of 15 whinchats, 10 of which gave complete traces of the annual cycle (i.e. winter to winter). The height of bars represents the latitudinal spread of each stage across all birds.

Table 6.1. Average values and results of paired *t*-tests and Wilcoxon matched pairs tests comparing spring and autumn migration. Note that the latitude of a given location depends upon the choice of sun elevation angle, here calculated from locations on both the wintering (SEA_W) and breeding (SEA_S) grounds. Sample sizes differ for spring and autumn due to uncertainty around the equinox corresponding to the timing of migration.

	Average (± SE)		
Aspect of migration	Spring	Autumn	*n spring/autumn*
Total migration time (days)	19.9 (±2.2)	44 (±3.8)	11 / 8
Migratory flight (days)	9.8 (±0.4)	10 (±1.3)	11 / 8
Number of stopovers	1.7 (±0.3)	3.8 (±0.2)	11 / 9
Total number of days at stopovers	11.8 (±2.2)	34.8 (±4.4)	11 / 9
Duration of stopovers (days)	7.2 (±0.8)	9.6 (±1.2)	15 / 9
Flight between stopovers (days)	3.6 (±0.4)	2.1 (±0.2)	15 / 8
Distance between stopovers (km):			
winter sun elevation angle	2241 (±162)	850 (±90)	14 / 8
summer sun elevation angle	2308 (±172)	775 (±105)	13 / 8
Flight speed (km/hr):			
winter sun elevation angle	27.4 (±1.4)	21.1 (±2.2)	14 / 8
summer sun elevation angle	29.7 (±1.8)	19.5 (±2.2)	13 / 8

	Spring vs. autumn migration			
	t / V	df / *n*	*p*	*Bonferroni* adjusted *p*
Total migration time	0	- / 8	**0.014**	0.010
Migratory flight (days)	-0.009	7 / 8	0.86	
Number of stopovers	-3.8	8 / 9	**0.0053**	**0.0056**
Total number of days at stopovers	0	- / 9	**0.014**	0.013
Mean duration of stopovers	-1.5	8 / 9	0.18	
Mean days flight between stops	3.9	7 / 8	**0.0061**	**0.0063**
Distance between stopovers	36	- / 8	**0.0078**	0.0083
Mean flight speed (km/hr):				
winter sun elevation angle	2.9	7 / 8	**0.023**	**0.017**
summer sun elevation angle	3.8	7 / 8	**0.0066**	**0.0071**

4. Age and sex differences

Tests of age and sex differences are presented in Table 6.2. There was no difference between males and females in the timing of departure from winter territories (difference = 1.6 days). First-winter birds departed on average eight days after adults but this difference was not significant, and results did not change if the last day south of the Sahara was used in place of the last day on territory (difference = 5.4 days). Total spring migration time did not differ between males and females, or between adults and first-winter birds (difference = 1.1 and 2.4 days, respectively). Males and females did not differ in their arrival date on the breeding grounds (difference = 3.1 days), but first-winter birds arrived on average eight days later than adults (Figure 6.7). Despite later arrival on the breeding grounds for first-winter birds, there was no significant age difference in the number of stopovers, the total number of days spent at stopovers, the average journey in days between stopovers, mean travel speed or the total distance travelled (considering locations from both winter and summer sun elevation angles when these differed), suggesting that small differences accumulated over the whole migration leading to later arrival for first year birds. Birds caught as first-winter or adults remained on the breeding grounds for a similar number of days, departed at similar times, and travelled back to the winter territory at similar speeds and in the same amount of time (Table 6.2).

Table 6.2. Results of *t*-tests and Wilcoxon tests comparing the different aspects of the migratory cycle according to the age and sex of individuals, plus further comparisons between first-winter and adult birds during spring migration to explore reasons for a difference in arrival time on the breeding grounds between these age groups. Note that the latitude of a given location depends upon the choice of sun elevation angle, here calculated from locations on both the wintering (SEA_W) and breeding (SEA_S) grounds. Comparisons are not made between sexes in some cases (-) due to insufficient data or sample sizes. Sample sizes are re ported in place of degrees of freedom (df) for Wilcoxon tests.

	1st winter vs. Adult					♂ vs. ♀			
Aspect of migration	*t* / W	df	*n* 1st w, ad	*p*	*Bonferroni* adjusted *p*	*t*	df	*n* ♂,♀	*p*
Time territory -> breeding	-0.5	8.7	5,6	0.60		-0.3	3	9,2	0.80
Time breeding -> territory	8		5,6	0.61		-	-	-	-
Last day on winter territory	1.7	8.4	9,5	0.13		-0.3	6.1	10,5	0.79
Last day south of Sahara	1.6	6.9	9,5	0.16		0.8	8.3	10,5	0.43
Arrival at breeding grounds	27		6,5	**0.034**	**0.0029**	0.5	1.3	9,2	0.70
Days on breeding grounds	-0.9	2.6	6,2	0.43		-	-	-	-
Depart from breeding grounds	0.1	4.2	6,2	0.91		-	-	-	-
	Spring migration								
Number of stopovers	18.5	-	6,5	0.55					
# days spent at stopovers	-0.7	8.5	6,5	0.47					
Mean days flight between stops	-1.1	12.0	9,5	0.28					
Number of days travelling	1.8	6.7	6,5	0.11					
Mean min flight speed (km/hr):									
winter SEA	-0.7	4.8	9,5	0.54					
summer SEA	15.5	-	8,4	1.00					
Mean distance between stops:									
winter SEA	-1.3	10.3	8,4	0.23					
summer SEA	-1.2	9.9	8,4	0.27					
Total distance travelled:									
winter SEA	0.02	5.1	6,5	0.98					
summer SEA	-0.5	3.5	6,4	0.64					

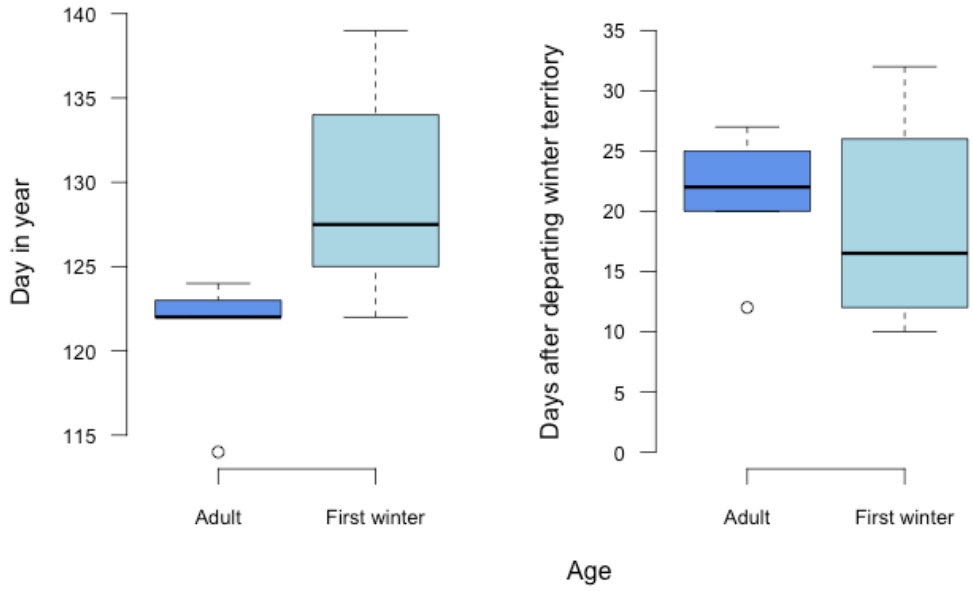

Figure 6.7. Arrival time on the breeding grounds in relation to age (adult or first-winter) in terms of Julian day (left) and number of days since departing the winter territory. First-winter birds arrived significantly later than adults at the breeding grounds (p = 0.034; Table 6.2).

6.5 Discussion

Migratory connectivity and evidence for a generalist migratory strategy

Breeding locations were spread over a range of c.1,500 km in longitude and c.850 km in latitude, showing that migratory connectivity occurred only at a large scale (i.e. >1,000 km), as predicted by the serial residency hypothesis (Cresswell, 2014): the stochastic nature of initial site selection within the wintering range during the first migration followed by high site fidelity in repeat migrations results in widely ranging wintering locations for any one breeding population, which in reverse results in the wide ranging breeding locations seen in this wintering population. Migratory connectivity on a large scale has been shown in several migrants (e.g. >1,000 km for common redstart *Phoenicurus phoenicurus* (Kristensen et al., 2013), c.2,000 km purple martin *Progne subis* (Fraser et al., 2012), and >3,000 km for great reed warblers *Acrocephalus arundinaceus* (Lemke et al., 2013); see Cresswell, 2014 for

more examples). For whinchats, lower site fidelity on the breeding grounds (Bastian, 1992; Bezzel and Stiel, 1977; Shitikov et al., 2012) may have further increased the scale of connectivity as individuals dispersed upon returning to breeding areas. The wide variation in spatial and temporal aspects of migration across individuals, combined with connectivity on a large scale, suggests a generalist migratory strategy, also in agreement with the serial residency hypothesis (Cresswell, 2014). From an evolutionary context, a generalist strategy allows a species to deal with a greater range of conditions during migration and upon reaching unknown wintering or breeding grounds.

Response to conditions during migration

During migration, birds travelled directly over the Sahara desert without a stopover greater than one day and travelled and faster than at other times during migration, as has been shown for other species (Tøttrup et al., 2012; Yohannes et al., 2009), most likely in response to a lack of suitable stopover sites. All birds had stopovers located immediately after this crossing, most likely as a strategy to replenish fat reserves, as seen in other migrants such as great reed warblers (Lemke et al., 2013). Stopovers were often situated immediately before the barrier crossing, most likely to accumulate sufficient fat reserves for non-stop flight. Stopover locations, duration and fat reserves upon departure have been linked to barrier width and location for many species (Biebach et al., 1986; Coiffait et al., 2011; Rubolini et al., 2002; Yom-Tov, 1984). Six individuals travelled to stopovers before crossing the Sahara after leaving the wintering territory, perhaps implying a shift to higher quality sites to aid pre-migratory fattening; however the fact that no dominance-based territory occupancy nor response to territory characteristics other than an adjustment of territory size (see Chapter 3: *Site fidelity* and Chapter 4: *Winter habitat*) and that some individuals departed for the crossing immediately from the winter territory suggests that wintering territories generally may be sufficient for pre-migratory fattening. It may be that birds make small stops to replenish reserves before the Sahara, although this degree of temporal resolution was beyond the scope of our methods. Most likely, these strategies promote survival during migration itself.

The lack of a relationship between departure and arrival times during spring migration further supports an influence of environmental conditions on total migration time. Arrival and departure times are frequently related to conditions experienced during migration itself (Drake et al., 2014; González-Prieto and Hobson, 2013; Gordo and Sanz, 2007), wintering conditions (Balbontin et al., 2009; González-Prieto and Hobson, 2013; Gordo and Sanz, 2007; Møller, 1994; Saino et al., 2004), body condition (Francis and Cooke, 1986; Lozano et al., 1996; Lundberg and Alatalo, 2010; Marra et al., 1998; Møller, 1990; Møller, 1994), and competition between conspecifics (Kokko, 1999). For pied flycatchers *Ficedula hypoleuca*, conditions encountered during migration influence the timing of breeding, for example (Both et al., 2006b). If none of these had an influence on migration, we would expect to see a direct relationship between departure and arrival times, but this was not the case.

Minimum flight speeds during migration were 28.6 ±1.8 km/hr in spring and 20.5 ±2.2 km/hr in autumn, equal to 676 and 488 km/day, respectively. This is within the range reported for small passerines (Bloch and Bruderer, 1982; Bruderer and Boldt, 2001), and not dissimilar to those reported in other migration studies, although figures vary widely: e.g. turtle doves *Streptopelia turtur*: 240 – 812 km/day (Eraud et al., 2013), purple martins: 450 km/day (Fraser et al., 2012), northern wheatears *Oenanthe oenanthe*: 290 km/day (Bairlein et al., 2012), Swainson's thrushes *Catharus ustulatus*: 123 – 537 km/day (Delmore et al., 2012), great reed warblers: 220 km/day in spring and 139 km/day in autumn (Lemke et al., 2013), common swift: 263 – 650 km/day (Åkesson et al., 2012), and red-backed shrike: 233 km/day in spring and 356 km/day in autumn (Tøttrup et al., 2012). Erni *et* al (2005) report 38 km/hr as an acceptable speed for small songbirds. Speeds over the Sahara were often at the higher end of these figures (Figure 6.5). Minimum fight speeds at this time may have been inflated due to the inherent inaccuracy of geolocator data (± c.200 km), or wind may have assisted flight more than was suggested from our analyses. Because precision regarding both wind and location data during migration was limited, our minimum flight speeds should be considered with a degree of uncertainty. Nevertheless, significantly higher speeds without tailwind assistance have been reported for great snipe *Gallinago media* of 54 – 97 km/hr (Klaassen et

al., 2011). Furthermore, although it is assumed that migrants such as whinchats do not usually fly during the day, daytime migration must occur during barrier crossings (Schmaljohann et al., 2007), perhaps explaining faster flight speeds. Flight ranges were also within those possible for small passerines (Hilgerloh and Wiltschko, 2000; Moreau, 1961).

In this study, wind assistance probably did not influence ground speed, which is surprising, given that migrants have been shown to adjust their behaviour according to wind conditions (Kemp et al., 2010; Newton, 2010b). Migratory routes over the Sahara did coincide with favourable wind patterns (e.g. see Figure 6.1 in Erni et al., 2005, plus online maps from NOAA/National Weather Service: Climate Prediction Center, 2014, and compare with Figures 6.1 and 6.2 in results) as has been shown for other migratory species (Barboutis et al., 2011), and such routes are hypothesised to be possible only with wind assistance (Erni et al., 2005). Although data on autumn migration routes were limited due to the equinox, the data we had suggested that whinchats undertook a loop migration, as has been found with other Palearctic migrants (Bairlein, 2001; Berthold, 2001; Kristensen et al., 2013; Tøttrup et al., 2012), involving a south-easterly route to the wintering grounds. This route follows favourable wind patterns and so most likely increases survival during migration (Erni et al., 2005). That wind assistance was not influential is therefore surprising, but may be due to several reasons. Firstly, migrants often adjust the timing of migration in response to ecological conditions and interrupt migration during adverse weather conditions (Alerstam, 1981; Delingat et al., 2007), and therefore whinchats may not have migrated when winds were unfavourable. The timing of departures with favourable wind conditions has been shown for northern wheatears (Delingat et al., 2007; Dierschke, 2003b), Eurasian blackcaps *Sylvia atricapilla* (Arizaga et al., 2011), black redstarts *Phoenicurus ochruros* (Morganti et al., 2011) and European robins *Erithacus rubecula* (Dänhardt and Lindström, 2001; Schaub et al., 2004; Tsvey et al., 2007), amongst others (e.g. see references within Chernetsov, 2012b; Elkins, 2004). Secondly, because geolocators only record birds that survive migration, if winds did indeed affect ground speeds to the extent where slower migration caused mortality, such as when crossing the Sahara, we would not record this. Thirdly, wind conditions

may have not reached a threshold where they influenced migration, as has been shown in whitethroats *Slyvia communis* (Fransson, 1998) and some populations of northern wheatears (Dierschke and Delingat, 2001). Nocturnal migrants have been shown to migrate without tailwind assistance (Karlsson et al., 2011), suggesting that wind may not strongly influence flight. Finally, it may be that wind assistance does influence ground speed, but that our method of using wind data from ground level combined with the inherent inaccuracy of geolocators prevented us from measuring this level of detail. It should be noted also that for we could only calculate minimum flight speeds and that these were inherently inaccurate due to the low precision of locations derived from geolocators.

Time allocation

Most time was spent on the wintering grounds and the least was spent migrating, as has also been found in other migrants such as common redstarts (Kristensen et al., 2013) and common swifts *Apus apus* (Åkesson et al., 2012). The study population of wintering whinchats has been shown to have high overwinter survival (see Chapter 5: *Survival*), as is also the case for many other long-distance migrants (Marra and Holmes, 2001; Sillett and Holmes, 2002); in fact, mortality can be 15 times greater during migration than stationary periods (Sillett and Holmes, 2002). Spending more time wintering is most likely a strategy to maximise survival, because the pressures and constraints of breeding, predation and overnight starvation associated with higher latitudes are absent on the wintering grounds. Consequently, by linking the time spent at each stage with likely survival during that stage, whinchats most likely increase their annual survival.

As predicted, spring migration was more rapid than autumn, in agreement with previous studies (e.g. see Fransson, 1995; Kristensen et al., 2013; Lemke et al., 2013; Tøttrup et al., 2012). Faster spring migration was because birds travelled at a higher velocity and stopped less frequently during spring, as has also been shown for other migrants (Karlsson et al., 2012), and not because stopovers were shorter in duration, as is the case for some Neotropical warblers (Morris et al., 1994) and great reed

warblers (Lemke et al., 2013). Some species, such as red-backed shrikes *Lanius collurio* (Tøttrup et al., 2012), travel faster during autumn migration, but this is likely due to their loop migration greatly extending the length of the spring migration. Migratory behaviour also varied less across individuals in spring regarding total migration time, the total number of days spent at stopovers, and departure and arrival dates. Despite limited data during autumn migration, migration routes and stopover locations were also less variable and more direct during spring, as is the case for common redstarts (Kristensen et al., 2013). Less variation during spring is most likely because delayed arrival on the breeding grounds holds the highest implications for future survival and reproduction, therefore limiting any flexibility during spring migration, especially if individuals are competing with each other for early arrival.

Age and sex differences in migratory behaviour

Generally, migratory phenology did not vary with age and sex. Later arrival on the breeding grounds for birds in their first winter, most likely because they left their winter territories later than adults, was the only difference between demographic groups. Slower migration for first-winter birds could also due to poorer feather quality for birds in juvenile plumage. We are only aware of one other study that has tracked juveniles during part of their first migration (McKinnon et al., 2014); however results agree with later arrival for first-winter birds documented for other migratory species (McKinnon et al., 2014; Newton, 2010a). Our low sample sizes may have prevented us from finding any differences, or it may be that demographic groups, especially males and females, do not vary in their migratory behaviour, as is supported by a lack of dominance-based habitat occupancy or wintering behaviour for whinchats (see Chapter 3: *Site fidelity* and Chapter 4: *Winter habitat*). Furthermore, any age differences should only occur during spring migration because all birds have completed one annual cycle by autumn, and differences may be much less after the first trip from the natal grounds. This may explain our finding of no age differences during autumn migration: effectively all birds were “adults” after reaching the breeding grounds.

Implications for migrant conservation

From a conservation perspective, large variation across individual migration strategies and generalist wintering requirements will result in greater flexibility to changing conditions or habitat loss for a species, and therefore more resilience to both anthropogenic and natural drivers of decline. If a particular stopover site is lost or unpredictable sources of mortality occur along a particular migratory route, for example, only a small proportion of the species should be affected. Yet despite large variation, some aspects of migration, such as migratory routes over the Sahara and the subsequent stopovers, were more similar across individuals, perhaps suggesting higher vulnerability to drivers of declines acting in these areas. Furthermore, extremely high site fidelity at the territory level on the wintering grounds despite variation in territory quality and characteristics (see Chapter 3: *Site fidelity* and Chapter 4: *Winter habitat*) suggests that faithfulness to stopover locations is also likely, possibly reducing flexibility to changing conditions despite a generalist strategy. Stopover site fidelity has been shown for many small passerine migrants such as garden warblers, blackcaps, Eurasian reed warblers and common chiffchaffs *Phylloscopus collybita*, amongst others (Barboutis et al., 2014; Cantos and Tellería, 1994; Yohannes et al., 2007). Furthermore, some individual whinchats in this study remained at stopover locations for as long as 13 days implying that environmental conditions experienced at staging areas can influence population dynamics (Eraud et al., 2013). Yet there is also evidence that Palearctic migrants may not be faithful to stopover locations (Catry et al., 2004b). Knowledge of which species are faithful to stopover sites and whether migrants are capable of switching stopover locations is crucial to determining their resilience to habitat loss.

In summary, we show low migratory connectivity and a generalist migratory strategy for whinchats, and provide evidence that migrants have several methods of adjusting their migratory behaviour in accordance to conditions experienced during migration, suggesting that whinchats may have some resilience to known drivers of decline.

CHAPTER 7: DISCUSSION

Despite the large role the non-breeding season can potentially play in shaping migrant populations, our knowledge of this fundamental and predominant part of the annual cycle is extremely limited, especially for the Palearctic system. This thesis studied the winter and migration ecology of a declining long-distance Palearctic migrant, the whinchat, in West Africa, exploring how events occurring outside of the breeding season may influence the population dynamics of whinchats and so potentially other Palearctic migrants that winter in Africa. By studying a migrant in detail on the wintering grounds, this research presents novel findings concerning the degree of winter site fidelity and habitat use in winter, the first estimates of overwinter and annual survival for whinchats from the wintering ground perspective, and for the first time reveals their migration routes and behaviour – some of the first documented for any small long-distance migrant from the wintering grounds.

We show that whinchats are highly site faithful both within and between winters, despite the potential for individuals to move territories within and between years; that site fidelity is not influenced by age or sex; and that whinchats are more faithful to their wintering grounds than their breeding grounds. That annual survival is not influenced by residency time in the previous winter suggests that some individuals may have multiple wintering sites. We document large variation in territory habitat characteristics and no evidence of dominance-based selection for territories; instead, individuals respond to the variation in habitat features at the territory-level, specifically the density of perching shrubs and crops, by adjusting their territory size and the areas they use most within their territories. We document very high overwinter survival, annual survival rates which are comparable to or higher than those documented on the breeding grounds, and no difference in survival according to age or sex. The study reveals migratory routes to and from the breeding grounds in Eastern Europe; the location of stopovers, including those in North Africa common across numerous individuals; and shows that migratory connectivity occurs only on a

large scale. Migration ecology and behaviour varies across individuals; demographics have little influence on migration ecology; flights over barriers demand faster migration speeds; and spring migration is faster and less variable than autumn migration.

7.1 Whinchats are generalists

The combination of 1) the large variation in many aspects of winter and migration ecology and behaviour and in habitat characteristics across individual territories; 2) extremely high site fidelity both within and between winters for resident individuals; 3) very high overwinter survival despite changing conditions as winter progresses; and 4) a lack of age or sex-based differences in winter ecology and all but one aspect of migration ecology and behaviour all strongly suggest that whinchats have a generalist migratory and wintering strategy within their wintering habitat of open savannah.

The large variation in habitat characteristics and land-use types, both on a spatial scale across territories and on a temporal scale within territories held throughout the winter, implies that whinchats are capable of utilising a wide range of ecological conditions during winter. With a non-specialist strategy, a good quality winter territory is most likely one that simply provides sufficient resources for survival during winter and across successive winters, and has at least some key features, specifically those that promote optimal foraging and the defence of key resources. The influence of perching shrubs and crops on territory size – whereby whinchats will use a smaller area if structural shrubs and crops are present and favour densely scrubbed areas within territories – plus the fact that perching shrub density was one of the features that remained unchanged throughout winter, suggest that the presence of perches are a key requirement for a winter territory. Generalist habitat requirements are most likely possible because of the diverse foraging strategy of whinchats, and the range of foraging strategies observed during the study (foraging on the ground, fly-catching, gleaning from vegetation) all require perches, as does territory defence to secure these resources. Previous research has highlighted the

importance of perches for foraging whinchats (Barshep et al., 2012; Hulme and Cresswell, 2012), and mirrors findings of the significance of these features for whinchats for both breeding territories (Bastian and Bastian, 1996; Fischer et al., 2012; Horch and Birrer, 2011; Labhardt, 1988; Oppermann, 1990) and stopover site selection (Koce and Denac, 2010). For these reasons, habitat structure is likely to be a surrogate for winter habitat quality for whinchats, and the findings of the above studies suggests that this is applicable during other stages of the annual cycle.

The benefits of a non-specialist wintering strategy and generalist requirements are numerous. Firstly, a generalist strategy increases the range of habitats and suitable territories within those habitats that are available for overwintering. These increase survival in the non-breeding season by increasing the probability that inexperienced individuals (i.e. first-winter birds undertaking their first migration) will arrive in suitable habitats and can remain there. Low migratory connectivity combined with high site fidelity in following winters suggests that the first migration and consequently stopover and winter site selection within the wintering range during the first winter is stochastic, as is predicted to be the case for small long-distance passerine migrants (Cresswell, 2014) – juveniles migrating for the first time have no prior experience of migratory routes and conditions, and the unpredictable nature of the first migration leads to the low migratory connectivity found, even if migratory routes have been determined to some extent by weather conditions and geography. Aside from those made immediately after leaving the winter territory but before commencing migration (i.e. stopovers likely used for pre-migratory fattening), stopovers also occurred after rather than before a barrier, as would be expected for first-winter birds with no prior knowledge of migration, and if surviving adults are then faithful to the same stopover locations in subsequent migrations. Having generalist requirements therefore grants flexibility and removes the need to continue migration in search of a suitable territory.

Secondly, if individuals can adapt to changing conditions, then they can benefit from both within and between year site fidelity. If conditions change throughout the winter – as we have shown they do – then birds can remain in their territories

without suffering reduced survival if they can acquire the resources they need to maintain condition over winter. By doing so, the costs of relocating are avoided. If wintering conditions change between years, individuals are able to return to and winter in the same territories held in previous winters. Both of these situations improve the probability of survival by increasing predictability and familiarity within and between years, and likely explain the very high degree of site fidelity found at both temporal scales. If a territory promotes overwinter survival, then the optimum strategy is to return to the same territory in future winters rather than risk relocating. If conditions change too much and survival is compromised, then the optimum strategy is to relocate, which would explain why some whinchats might have multiple wintering areas. Because birds wintering for the first time do not have any experience of how much conditions may change during winter, inevitably some individuals will occupy territories where conditions change to the degree where survival becomes compromised. These birds must then relocate, and therefore multiple wintering sites are necessary. These individuals are far from nomadic and still benefit from within and between-year site fidelity, as is highlighted by their short-term winter residency and the fact that they were just as likely to return in subsequent winters.

Thirdly, if individuals can maintain adequate body condition under a range of conditions – especially if fewer reserves are needed for optimal body condition, as is suggested to be the case during winter by the fact that almost all individuals captured throughout winter had very minimal fat reserves (see Risely et al., 2014 for a detailed account of body mass during winter for whinchats) – and winter territory quality is defined simply by whether its resident can survive over the winter, then a large number of territories are likely to be of sufficient quality. Consequently, the need to compete for territories (other than to reoccupy a previous territory) is removed. The lack of any dominance-based territory occupancy indeed suggests that individuals do not compete for territories based on differing habitat characteristics, and suggests that the benefits of site fidelity outweigh those of competing for a 'better' territory. This should be the case if optimum body condition is easily maintained in a range of conditions and if any territory with key features is an

adequate territory. If territory quality is determined to some extent by the availability of perching structures because of their use for foraging and territory defence, individuals may simply compensate for the variation in these features by adjusting their territory size. With this strategy, birds can quickly establish a territory upon arrival, and so can allocate time and energy more efficiently to replenishing reserves after migration and maintaining condition over the winter.

Yet some form of intraspecific competition must exist if returning adults are to reoccupy last winter's territory given that a large number of first-winter birds are arriving without a pre-established territory and may wish to occupy territories that are already claimed. Whinchats were often seen to interact in an aggressive and territorial manner, especially at the start of the wintering season. Intraspecific competition most likely reflects the importance of site fidelity rather than competition for territories of varying quality. Because all returning birds reoccupy their previous territories, the only competitors for returning adults must be juveniles arriving on the wintering grounds for the first time. For returning adults, the benefits of site fidelity urge displacing any newly arrived first-winter birds occupying their old territory. For juveniles, the benefits of competing with more dominant birds are likely to be few if territories do not vary significantly in quality, especially if they can compensate for poorer territory quality by increasing territory size. Because generalist requirements should mean that winter territories are plentiful, juveniles should be able to relocate nearby, therefore avoid the costs of relocating significant distances. Perhaps this explains why whinchats appear to be grouped within large areas of seemingly suitable habitat. With survival rates of c.50%, half of any adult territories are not reoccupied in a winter so these spaces are available for juveniles. This then raises the suggestion that juveniles may then seek out adults because they indicate an area of suitable habitat quality. Territorial interactions are then inevitable as juveniles find the empty territories and their boundaries within these areas. This would reinforce initial stochasticity in habitat selection and lead to clustering due to a "colonisation" event some years in the past.

Generalist habitat requirements in the non-breeding season would explain the variation in migratory behaviour across individuals, such as the variation in stopover locations, migratory routes and breeding locations, and in the decision to either depart directly from the wintering territory or to stopover before crossing the Sahara. By having a generalist strategy, birds can adjust and tailor their individual migratory strategies to meet their individual energetic demands, some of which may be determined by the nature of their winter territories. This seems most likely considering the relationships between body condition and the success of migration and future breeding success documented for other migrants (e.g. Bauchinger et al., 2008; Norris, 2005; Norris et al., 2004; Norris and Marra, 2007; Sandberg and Moore, 1996; Smith and Moore, 2003; Smith and Moore, 2005). That some individuals are able to fatten for migration on their winter territories – as the fact that over half of tracked birds appear to depart for the Sahara crossing directly from the winter territory implies – further suggests that individuals are able to tailor their migratory strategies to their individuals needs.

7.2 The role of the non-breeding season in population dynamics

The findings of this study suggest that the winter period itself does not significantly limit whinchat populations. Firstly, overwinter survival was extremely high, suggesting that there are few pressures on individuals during winter itself. Many aspects of winter habitat and winter ecology varied widely across individuals: if conditions during winter were limiting, we may expect to see less variation in aspects such as habitat characteristics across individual territories, because individuals should favour the features beneficial for survival and avoid those that are not. This was not the case. Secondly, site fidelity was very high both within and between winters and there was no evidence of dominance-based winter habitat occupancy. This suggests that winter habitat has few carry-over effects on future survival and reproduction: if winter habitat is limiting and has significant carry-over effects, we would expect selection to favour competition between individuals for higher quality territories, as has been shown in some other migrants, particularly in the Neotropics (e.g. Marra, 2000; Marra and Holmes, 2001), or perhaps individuals

to relocate to 'better' territories both within and between years. Neither of these occurred. The lack of age and sex differences in many aspects of winter and migration ecology and behaviour implies that no particular demographic group is more susceptible to wintering conditions, reducing the possibility of skewed population dynamics and so the influence of the winter season. Thirdly, most of the annual cycle was spent on the wintering grounds, as would be expected if individuals are maximising their survival by spending the most time where their survival is greatest. Most likely, whinchats reduce the influence of wintering conditions on survival and population dynamics by having generalist wintering requirements.

Consequently, to explain annual return rates of 54%, mortality must be highest outside of the wintering period, i.e. during active migration or the breeding season. Annual return rates measured on the breeding grounds are similar to those we report here in Africa, and survival during the breeding season is still high, and certainly higher than annual return rates. Therefore, if high mortality is not occurring during winter (as we show it is not) and mortality during the breeding season does not explain annual survival rates (as it does not), the highest mortality must be during migration itself. This reflects findings for other species (details in above chapters), although research is lacking (Sillett and Holmes, 2002). Fundamentally, annual survival is highest when measured on the wintering grounds, and overwinter survival is both very high and does not differ with age, suggesting that juvenile birds on their first migratory flight (i.e. what from Europe to Africa) have the highest mortality. This also explains why we also see no effect of age on annual return rates to the wintering grounds. Any age differences occurring during the very first migration would not be recorded from the wintering grounds. On departing for spring migration, juveniles have effectively become adults – they have completed one successful migration and survived during winter – and therefore their survival during migration to the breeding grounds is comparable to that of older adults that have migrated before. If the lower survival often reported for juveniles was occurring elsewhere, for example on the return migration to the breeding grounds, then this would be reflected in lower winter return rates for first-winter birds, but this was not the case. Furthermore, a lack of any difference in survival between age

classes during the second migration suggests that prior knowledge of stopover sites during this journey (which only adults that have completed at least one full migration should have) is likely to be less important for survival during migration. If this were the case we should see differential survival for adults and juveniles, but we did not. This would suggest that prior knowledge of stopover sites is not important for the first migratory flight from Europe to Africa, and this then suggests that higher mortality for juveniles is a result of the relative stochasticity of migration and winter site selection upon arrival. A lack of knowledge and experience results in a greater proportion of juveniles arriving in unsuitable habitats, and therefore higher mortality. The consequences of this are likely increasing as habitat degradation in Africa increases and so, likely contributing to the declines of long-distance migrants. Species which favour or tolerate the increasing anthropogenic habitat modification that is occurring in sub-Saharan Africa (Bourn and Wint, 1994), such as whinchats, may be an exception. This suggests that population declines in these species are a result of deteriorating conditions in Europe, which is indeed supported by studies of breeding whinchats (e.g. Britschgi et al., 2006; Broyer, 2009; Müller et al., 2005).

7.3 Are whinchats a model species or an exception?

Current research suggests that, especially for Palearctic migrants, a generalist wintering and migratory strategy is relatively typical. High site fidelity both within and between years is prevalent in both Palearctic and Neotropical migrants (Cantos and Tellería, 1994; Catry et al., 2003; Cresswell, 2014; Cuadrado, 1995; Holmes and Sherry, 1992; King and Hutchinson, 2001; Koronkiewicz et al., 2006; Kricher and Davis, 1986; Latta and Faaborg, 2001; Newton, 2010b; Skilleter, 1995; Wunderle Jr and Latta, 2000). Recent studies have found that only large-scale migratory connectivity occurs for a number of other migrants (e.g. Fraser et al., 2012; Kristensen et al., 2013; Lemke et al., 2013). The general absence of strong competition with resident species during winter (Greenberg, 1986; Leisler, 1992; Salewski et al., 2003), diverse foraging strategies (Salewski et al., 2002a, 2003), and occurrence across a wide range of habitats of varying quality, some of which are degraded (e.g. Hulme and Cresswell, 2012; Stevens et al., 2010; Wilson and

Cresswell, 2010a; Wilson and Cresswell, 2010b, 2006) further support that long-distance migrants are typically generalists. Here, unexpectedly significant demographic differences in migratory behaviour did not occur, the only difference being the later arrival of first-winter birds to the breeding grounds. If age and sex related differences are indeed absent, whinchats may be at the far end of the generalist-specialist scale with very broad requirements. More detailed studies of departure and arrival dates are needed to establish whether this is the case for whinchats.

Contrasts appear when comparing the Palearctic and Neotropical systems. Palearctic migrants may be much more generalist that Neotropical migrants. In the Neotropics, demographic differences, dominance-based habitat occupancy, declines in body condition relating to habitat quality during the wintering period, carry-over effects between winter and the breeding season, and strong migratory connectivity are frequently documented (e.g. Cormier et al., 2013; Macdonald et al., 2012; Marra, 2000; Marra and Holmes, 2001; Norris, 2005; Reudink et al., 2009; Rockwell, 2013; Sherry and Holmes, 1996). We propose that many of these differences are, at least to some extent, the consequence of less available land area and its clumped distribution into islands in the Caribbean in mid-latitudes, plus generally shorter migration distances for Neotropical wintering migrants (Greenberg and Marra, 2005). This acts to reduce the availability of suitable wintering habitat, increases the potential for and benefits of competition with conspecifics, also results in higher migratory connectivity, and consequently results in the non-breeding season having a larger role in shaping migrant population dynamics.

7.4 Study implications

Implications for the conservation of whinchats

Similar to many long-distance migrants, whinchats are declining. Through this study we have determined, or at least suggested, where mortality is occurring; the influence of wintering conditions and age and sex on population dynamics; and the

migratory routes, stopovers, behaviour and breeding locations of a typical wintering population, all of which are fundamental to the long-term conservation of whinchats. We have shown that the wintering period itself likely has limited influence on population dynamics; instead, the breeding period and specifically migration itself contribute most to declines, as is confirmed for whinchats by other studies both on the breeding and wintering grounds (e.g. Barshep et al., 2012; Britschgi et al., 2006; Broyer, 2009; Horch and Birrer, 2011; Hulme and Cresswell, 2012; Müller et al., 2005; Oppermann, 1990; Orlowski, 2004). Our results also support the importance of wind patterns and geography on shaping migratory pathways and stopover locations. Fundamentally, evidence suggests that migration itself is most limiting for first-winter birds undertaking their first migration; however exactly how and where mortality is occurring during migration is not clear without the ability to track birds that do not survive (see below).

Importantly, the findings throughout this study suggest that whinchats have some resilience to habitat change, both natural and anthropogenic. Firstly, territories were maintained throughout winter even though habitat characteristics changed significantly. Secondly, the majority of whinchats had established territories both in human-modified habitats and where there was at least some degree of continuing disturbance and anthropogenic habitat modification such as farming, grazing, or chopping for firewood, most of which changed in intensity throughout the winter. Furthermore, maize crops appear to be beneficial – whinchats established territories in or close to maize fields and territories were smaller if maize was present. A decrease in territory size suggests that maize provides more resources per unit area and is a high quality habitat. Although we did not compare whinchat densities in natural and modified habitats, densities were often lower – and certainly not higher – in unmodified habitats, and territories were available close to those established in farmland (per. obs but see also Hulme and Cresswell, 2012), suggesting that it is not simply a lack of habitat availability driving whinchats into these areas. Consequently, Whinchats may have some resilience to the increase in anthropogenic habitat modification predicted to occur in Africa. Most likely, generalist wintering requirements permit this high tolerance and adaptability. By being generalists,

whinchats are flexible to changing conditions, are not influenced by habitat variation at the demographic level, and show a tolerance or preference for some anthropogenic habitat modification and disturbance. Our findings suggest that some farmed or grazed land may even create higher quality wintering habitat.

Crucially, migratory connectivity occurred on a large scale, a pattern most likely to be reflected across other wintering and breeding populations. Consequently, any conservation actions aimed at the species-level should be on at least a regional or country-wide scale, because any single breeding population will be influenced by conditions occurring across a large area of the wintering range, and vice-versa for wintering populations. Despite the limited influence of the wintering period on population dynamics this study suggests, it is likely that the widespread habitat loss and degradation occurring in Africa is influencing whinchats to some extent throughout their breeding range, and the scale of migratory connectivity reveals that this impact will be wide-ranging. Combined with the well-documented drivers of declines acting on the breeding grounds (e.g. Britschgi et al., 2006; Broyer, 2009; Fischer et al., 2012; Horch and Birrer, 2011; Müller et al., 2005; Orlowski, 2004; Tome and Denac, 2012), whinchat declines are likely to continue. Migratory connectivity on a large scale may, however, grant some resilience to some processes acting in local areas (even on the scale of tens of kilometres), because fewer individuals will be affected from any single breeding or wintering population. If migratory connectivity were greater, the reverse would occur, and a large number of individuals from any one breeding population would be affected by events occurring in a single wintering location, and likewise for any wintering population.

Implications for the conservation of migrants

Even without anthropogenic influences, conditions in the non-breeding season are variable both within and between years (Pearson and Lack, 1992). Similar migratory species may thus have to share the flexibility and tolerance that this typical long-distance migrant has to changing conditions and anthropogenic habitat change and disturbance. Typically, migrants must be capable of coping with varying conditions

throughout their annual cycle, and so must be adaptable to some extent. Site selection is likely based on sufficiency rather than optimality, because finding and tracking the most optimal habitat is likely both unnecessary to maintain condition over winter and carries additional costs of moving. The degree of flexibility is, however, likely to be species and population-specific, as is shown by the variation in population trends seen within and between migrant species. Huge population crashes have been documented for some species when conditions have changed beyond their ability to adapt (Cowley, 1979; Winstanley et al., 1974). With the severity and frequency of extreme weather events and habitat degradation predicted to increase in Africa due to climate change and human population growth (Collier et al., 2008; Fauchereau et al., 2003; Nicholson et al., 2000; Tilman et al., 2002; Tilman et al., 2001), the influence of the non-breeding season on migrant population dynamics is likely to increase. Even if migrants have generalist requirements, the amount of unsuitable habitat is likely to increase. Likely the impact of any habitat change and degradation depends upon how specialist or generalist a species is, and where they lie on the continuum of low migratory connectivity due to high stochasticity during migration, or high migratory connectivity and low stochasticity. Both will determine whether conservation efforts should be based upon the preservation of key sites or habitat preservation on a large scale, or should focus on species and populations or take a multi-species approach. Determining migrants' thresholds of flexibility and tolerance to changing conditions and when natural population fluctuations are exceeded by anthropogenic influences are key for their conservation.

7.5 Study limitations and further research

Study limitations

This study is not without its limitations. When exploring site fidelity and survival, we would have been unable to detect large-scale dispersal (>5 km); however evidence suggests that if this did occur then it was slight and therefore unlikely to alter our findings. The lack of dominance-based habitat occupancy may be because we failed

to identify and measure the habitat characteristics that differed between age and sex classes; however considering that habitat features were explored on both a large and small-scale and the lack of age and sex differences throughout the study we are confident that there is indeed a lack of dominance-based ecology in this system. Our measures of body condition come from a single 'snapshot' at the time of capture, limiting our ability to explore the influence of winter habitat on body condition. Consequently, we were unable to explore carry-over effects in detail. One inherent problem with comparing the degree of site fidelity between breeding and winter periods is that dispersal is often higher on breeding grounds, leading to underestimates of survival. Nevertheless, the lack of age and sex differences in return rates to the wintering grounds still holds true, and therefore so does our belief that mortality is higher during the first migratory journey. We cannot dismiss the fact that geolocators are an inherently imprecise method for tracking individuals; yet even accounting for this we still show that migratory connectivity occurred only on a large scale. We feel that the scale of precision recorded was adequate for addressing the hypotheses explored.

Future directions

Considering the increase in habitat loss and degradation predicted due to anthropogenic influences and climate change, finding the thresholds that migrants must pass before changing conditions seriously impact on survival is likely to be fundamental to their conservation. Likewise, establishing whether site faithful species can redistribute if habitat degradation exceeds these thresholds, and at what spatial scale this may occur, should inform whether habitat preservation should focus at the site or regional level. Again, this is likely to be largely dependent upon the degree to which a species is a winter generalist or specialist and how this influences the survival of juveniles arriving in Africa for the first time. If specialist, the potential to redistribute is lower because individuals arriving in unsuitable habitat will have lower survival if they cannot redistribute. In this case, site-specific conservation will be key. Such an example might be the aquatic warbler *Acrocephalus paludicola* (Schäffer et al., 2006). If a species is more generalist,

individuals arriving in degraded areas or returning to a degraded territory will more likely find suitable conditions nearby or will be able to survive anyway in these degraded areas. In this case, the wintering distribution may fluctuate but population trends may not change significantly. Understanding the scale at which this occurs is key to focussing conservation efforts elsewhere, for example whether sites should be preserved locally or elsewhere.

Considering that some whinchats appear to have multiple wintering sites, further work is needed to establish both the thresholds at which individuals move, and how many additional sites these individuals may have if this is indeed one wintering strategy. Because no birds relocated a short distance, individuals must have relocated at least 5 km (i.e. beyond the study area boundaries). Why individuals would move such a distance, especially considering the costs of relocating and that winter habitat (and therefore winter territories) appears to be plentiful, is unknown. Perhaps there are tendencies for some breeding populations to move throughout winter, perhaps in response to the degree of habitat or climatic change within and between years in Africa, or temporal changes in resource availability. The number of individuals involved in such movements may also fluctuate. Perhaps this strategy increases population resilience by increasing variation in migratory strategies and therefore flexibility at the species level to unpredictable conditions. Determining large movements would be possible by tracking of individuals during winter, but currently only if movements exceeded the inherent inaccuracy of locations determined from geolocators or other tracking devices.

We established the degree of fidelity on the wintering grounds, but the degree of fidelity to individual migratory routes and stopovers between years is still unknown because it requires the repeat tracking of individuals and at a much better spatial resolution than given by geolocators. This was beyond the timescale and technology used in this study. Although we infer that mortality is highest during active migration, exactly where, when and how mortality occurs during this time – during flight, at stopovers, as a consequence of weather or the loss or degradation of stopover habitats – remains unanswered. Because we could 1) only track those

individuals that survived, and 2) not easily establish the influence that adding geolocators may have on migratory behaviour, we may have unrepresentatively sampled whinchat migration ecology. Determining where mortality is occurring during migration requires not only detailed studies of stopover ecology, but also fundamentally the ability to determine the location, timing and cause of mortality for individuals that do not survive. Currently no method exists for tracking small passerines over large distances that do not survive to be recaptured (see Strandberg et al., 2009 for non-passerines). Nevertheless, establishing the fate of these individuals is a key link in the chain of understanding migrant declines.

7.6 Study conclusion

To summarise: this thesis presents novel and significant research on the wintering and migration ecology of a declining Palearctic migrant, much of which is likely to be applicable to other declining species that winter in Africa. By being winter generalists, whinchats reduce the influence of the non-breeding season on survival and future reproduction and so on population dynamics: they are flexible and adaptable to changing conditions and variation in habitat characteristics, and appear to tailor their winter and migration strategies for optimal survival. Generalist wintering requirements have most likely evolved due to the predited stochastic nature of migration and site selection in the first winter, and allow individuals to benefit from high site fidelity in both current and subsequent winters. Generalist requirements grant some tolerance and resilience to the anthropogenic habitat modification occurring in Africa, but fundamental information regarding the thresholds of this tolerance and other information key understanding migrant declines, such as the fate of individuals that do not survive, is still missing.

CHAPTER 8: REFERENCES

Abdi, H., and L. J. Williams. 2010. Principal component analysis. Wiley Interdisciplinary Reviews: Computational Statistics 2: 433-459.

Aebischer, A., N. Perrin, M. Krieg, J. Studer, and D. R. Meyer. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. J. Avian Biol. 27: 143-152.

Ahola, M. P., T. Laaksonen, T. Eeva, and T. Lehikoinen. 2007. Climate change can alter competitive relationships between resident and migratory birds. J. Anim. Ecol. 76: 1045-1052.

Åkesson, S. 1993. Coastal migration and wind drift compensation in nocturnal passerine migrants. Ornis Scandinavica: 87-94.

Åkesson, S., and A. Hedenström. 2000. Wind selectivity of migratory flight departures in birds. Behav. Ecol. Sociobiol. 47: 140-144.

Åkesson, S., and A. Hedenström. 2007. How migrants get there: migratory performance and orientation. Bioscience 57: 123-133.

Åkesson, S., R. Klaassen, J. Holmgren, J. W. Fox, and A. Hedenström. 2012. Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators. PloS one 7: e41195.

Åkesson, S., G. Walinder, L. Karlsson, and S. Ehnbom. 2002. Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. J. Avian Biol. 33: 349-357.

Aldrich, T. W., and D. G. Raveling. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. The Auk 100: 670-679.

Alerstam, T. 1981. The course and timing of bird migration. In: D. J. Aidley (ed.) Animal migration. p 9-54. Cambridge University Press, Cambridge, UK.

Alerstam, T. 1993. Bird migration. In: P. Berthold, E. Gwinner and E. Sonnenschein (eds.) Avian migration. p 253-267. Springer Verlag, New York.

Alerstam, T. 2001. Detours in Bird Migration. J. Theor. Biol. 209: 319-331.

Alerstam, T. 2003. Bird migration speed Avian migration. p 253-267. Springer.

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos 103: 247-260.

Alerstam, T., and G. Högstedt. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. Ornis Scandinavica: 25-37.

Alerstam, T., and Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: E. Gwinner (ed.) Bird migration: physiology and ecophysiology. p 331-351. Springer Berlin Heidelberg.

Amrhein, V., H. P. Kunc, R. Schmidt, and M. Naguib. 2007. Temporal patterns of territory settlement and detectability in mated and unmated Nightingales *Luscinia megarhynchos*. Ibis 149: 237-244.

Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. Conserv. Biol. 19: 66-74.

Andriaensen, F., and A. A. Dhondt. 1984. Dynamics of a Robin population outside the breeding season. Bird Study 31: 69-75.

Arizaga, J., D. Alonso, and E. Barba. 2010. Patterns of migration and wintering of Robins *Erithacus rubecula* in northern Iberia. Ringing Migr. 25: 7-14.

Arizaga, J., E. J. Belda, and E. Barba. 2011. Effect of fuel load, date, rain and wind on departure decisions of a migratory passerine. J. Ornithol 152: 991-999.

Artem'ev, A. V. 2004. Molt and nest overlapping in long-distant migrants: main regularities of plumage replacement in the pied flycatcher, *Ficedula hypoleuca* (Passeriformes, *Muscicapidae*), from Karelia. Zoologichesky Zhurnal 83: 1127-1137.

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in the eastern North America. Current Ornithology 7: 1-57.

Bächler, E. et al. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. Plos One 5: e9566.

Baillie, S. R., and W. J. Peach. 1992. Population limitation in Palearctic-African migrant passerines. Ibis 134: 120-132.

Bairlein, F. 1985a. Body weights and fat deposition of Palaearctic passerine migrants in the central Sahara. Oecologia 66: 141-146.

Bairlein, F. 1985b. Efficiency of food utilization during fat deposition in the long-distance migratory garden warbler, *Sylvia borin*. Oecologia 68: 118-125.

Bairlein, F. 1991. Body mass of Garden Warblers (*Sylvia borin*) on migration: a review of field data. Vogelwarte 36: 48-61.

Bairlein, F. 1992. Recent prospects on trans-Saharan migration of songbirds. Ibis 134: 41-46.

Bairlein, F. 2001. Results of bird ringing in the study of migration routes and behaviour. Ardea 89: 7-19.

Bairlein, F., P. Beck, W. Feiler, and U. Querner. 1983. Autumn weights of some Palaearctic passerine migrants in the Sahara. Ibis 125: 404-407.

Bairlein, F. et al. 2012. Cross-hemisphere migration of a 25 g songbird. Biol. Lett. 8: 505-507.

Bairlein, F., and U. Totzke. 1992. New aspects on migratory physiology of trans-Saharan passerine migrants. Ornis Scandinavica 23: 244-250.

Baker, M., N. Nur, and G. R. Geupel. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using wrentits. The Condor 97: 663-674.

Balbontin, J. et al. 2009. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. J. Anim. Ecol. 78: 981-989.

Barboutis, C., I. Henshaw, C. Kullberg, S. Nikolopoulou, and T. Fransson. 2014. Fuelling in front of the barrier - are there age based behavioral differences in Garden Warblers *Sylvia borin*? PeerJ 2: e319.

Barboutis, C., I. A. N. Henshaw, M. Mylonas, and T. Fransson. 2011. Seasonal differences in energy requirements of Garden Warblers *Sylvia borin* migrating across the Sahara desert. Ibis 153: 746-754.

Barg, J. J., D. M. Aiama, J. Jones, R. J. Robertson, and K. Yasukawa. 2006. Within-territory habitat use and microhabitat selection by male Cerulean Warblers (*Dendroica cerulea*). The Auk 123: 795-806.

Barshep, Y., U. Ottosson, J. Waldenstroem, M. Hulme, and S. Svensson. 2012. Non-breeding ecology of the Whinchat *Saxicola rubetra* in Nigeria. Ornis Svec. 22: 25-32.

Barta, Z. et al. 2008. Optimal moult strategies in migratory birds. Philosophical Transactions of the Royal Society B-Biological Sciences 363: 211-229.

Bartoń, K. 2012. MuMIn: multi-model inference. R package version 1.

Bastian, A., and H. V. Bastian. 1996. Das Braunkehlchen: Opfer der ausgeräumten Kulturlandschaft. Aula, Wiesbaden.

Bastian, H. V. 1992. Breeding and natal dispersal of Whinchats *Saxicola rubetra*. Ringing Migr. 13: 13-19.

Bates, J. M. 1992. Winter territorial behavior of Gray Vireos. Wilson Bull. 104: 425-433.

Bauchinger, U., and H. Biebach. 2006. Transition between moult and migration in a long-distance migratory passerine: organ flexibility in the African wintering area. J. Ornithol 147: 266-273.

Bauchinger, U., T. Van't Hof, and H. Biebach. 2008. Migratory stopover conditions affect the developmental state of male gonads in garden warblers (*Sylvia borin*). Horm. Behav. 54: 312-318.

Bauchinger, U., T. Van't Hof, and H. Biebach. 2009. Food availability during migratory stopover affects testis growth and reproductive behaviour in a migratory passerine. Horm. Behav. 55: 425-433.

Bauchinger, U., A. Wohlmann, and H. Biebach. 2005. Flexible remodeling of organ size during spring migration of the garden warbler (*Sylvia borin*). Zoology 108: 97-106.

Bayly, N. J. 2007. Extreme fattening by sedge warblers, *Acrocephalus schoenobaenus*, is not triggered by food availability alone. Anim. Behav. 74: 471-479.

Bearhop, S., G. M. Hilton, S. C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society B: Biological Sciences 271: S215-S218.

Belda, E. J., E. Barba, and J. S. Monros. 2007. Resident and transient dynamics, site fidelity and survival in wintering Blackcaps *Sylvia atricapilla*: evidence from capture-recapture analyses. Ibis 149: 396–404.

Bennet, P. M., and I. P. F. Owens. 2002. Evolutionary ecology of birds. Oxford University Press, Oxford, United Kingdom.

Bensch, S., and D. Hasselquist. 1991. Territory infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. J. Anim. Ecol. 60: 857-871.

Bensch, S., D. Hasselquist, A. Hedenström, and U. Ottosson. 1991. Rapid moult among palaearctic passerines in West Africa - an adaptation to the oncoming dry season? Ibis 133: 47-52.

Benson, T. J., and J. C. Bednarz. 2010. Relationships among survival, body condition, and habitat of breeding Swainson's Warblers. Condor 112: 138-148.

Berthold, P. 2001. Bird migration: a general survey. Oxford University Press, USA.

Berthold, P., W. Fiedler, R. Schlenker, and U. Querner. 1998. 25-year study of the population development of central European songbirds: a general decline, most evident in long-distance migrants. Naturwissenschaften 85: 350-353.

Bezzel, E., and K. Stiel. 1977. The biology of the whinchat *Saxicola rubetra* in the bavarian alps. Anzeiger der Ornithologischen Gesellschaft in Bayern 17: 1-9.

Bibby, C. J., and R. E. Green. 1981. Autumn migration strategies of reed and sedge warblers. Ornis Scandinavica 12: 1-12.

Bibby, C. J., R. E. Green, G. R. M. Pepler, and P. A. Pepler. 1976. Sedge Warbler migration and reed aphids. Br. Birds 69: 384-399.

Biebach, H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. Experientia 41: 695-697.

Biebach, H. 1990. Strategies of trans-Sahara migrants. In: E. Gwinner (ed.) Bird migration. p 352-367. Springer, Berlin Heidelberg.

Biebach, H. 1998. Phenotypic organ flexibility in Garden Warblers *Sylvia borin* during long-distance migration. J. Avian Biol. 29: 529-535.

Biebach, H., W. Friedrich, and G. Heine. 1986. Interaction of bodymass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. Oecologia 69: 370-379.

BirdLife International. 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife Conservation Series No. 12.

BirdLife International. 2014. Species factsheet: *Saxicola rubetra*. Downloaded from http://www.birdlife.org Accessed 5th November 2014.

Blake, J. G., G. J. Niemi, and J. M. Hanowski. 1992. Drought and annual variation in bird populations: effects of migratory strategy and breeding habitat. In: J. M. Hagan, III and D. W. Johnston (eds.) Ecology and conservation of neotropical migrant landbirds. . p 419-429. Smithsonian Institution Press, Washington, D.C.

Blem, C. R. 1980. The energetics of migration. In: J. Gauthreaux (ed.) Animal migration, orientation, and navigation. p 175-224. Academic Press, New York.

Bliese, P. 2013. Multilevel Modeling in R (2.2) - A brief Introduction to R, the multilevel package and the nlme package.

Bloch, R., and B. Bruderer. 1982. The air speed of migrating birds and its relationship to the wind. Behav. Ecol. Sociobiol. 11: 19-24.

Böhning-Gaese, K. 1992. Ursachen für Bestandseinbußen europäischer Singvögel: eine Analyse der Fangdaten des Mettnau-Reit-Illmitz-Programms. J. Ornithol 133: 413-425.

Böhning-Gaese, K., and H. G. Bauer. 1996. Changes in species abundance, distribution, and diversity in a central European bird community. Conserv. Biol. 10: 175-187.

Böhning-Gaese, K., and R. Oberrath. 2003. Macroecology of habitat choice in long-distance migratory birds. Oecologia 137: 296-303.

Bolshakov, C., V. Bulyuk, and N. Chernetsov. 2003. Spring nocturnal migration of Reed Warblers *Acrocephalus scirpaceus*: departure, landing and body condition. Ibis 145: 106-112.

Bolshakov, C. V., and S. P. Rezvyi. 1998. Time of nocturnal flight initiation (take-off activity) in the European Robin *Erithacus rubecula* during spring migration: visual observations between sunset and darkness. Avian Ecology and Behaviour 1: 37-49.

Börger, L. et al. 2006. Effects of sampling regime on the mean and variance of home range size estimates. J. Anim. Ecol. 75: 1393-1405.

Both, C., R. G. Bijlsma, and M. E. Visser. 2005. Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. J. Avian Biol. 36: 368-373.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006a. Climate change and population declines in a long-distance migratory bird. Nature 441: 81-83.

Both, C., and L. T. Marvelde. 2007. Climate change and timing of avian breeding and migration throughout Europe. Clim. Res. 35: 93-105.

Both, C. et al. 2006b. Pied Flycatchers *Ficedula hypoleuca* travelling from Africa to breed in Europe: differential effects of winter and migration conditions on breeding date. Ardea 94: 511-525.

Both, C. et al. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B-Biological Sciences 277: 1259-1266.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 296-298.

Boulet, M., H. L. Gibbs, and K. A. Hobson. 2006. Integrated analysis of genetic, stable isotope, and banding data reveal migratory connectivity and flyways in the northern yellow warbler (*Dendroica petechia*; aestiva group). Ornithological Monographs 61: 29-78.

Bourn, D., and W. Wint. 1994. Livestock, land use and agricultural intensification in sub-Saharan Africa. Overseas Development Institute (ODI), London.

Bozdogan, H. 1987. Model selection and Akaike's information criterion (AIC): The general theory and its analytical extensions. Psychometrika 52: 345-370.

Bridge, E. S. et al. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. J. Field Ornithol. 84: 121-137.

Britschgi, A., R. Spaar, and R. Arlettaz. 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. Biol. Conserv. 130: 193-205.

Brodin, A. 2007. Theoretical models of adaptive energy management in small wintering birds. Philosophical Transactions of the Royal Society B: Biological Sciences 362: 1857-1871.

Brooke, M. D. L. 1979. Differences in the quality of territories held by wheatears (*Oenanthe oenanthe*). The Journal of Animal Ecology 48: 21-32.

Brown, D. R., and J. A. Long. 2007. What is a winter floater? Causes, consequences, and implications for habitat selection. The Condor 109: 548-565.

Brown, D. R., P. C. Stouffer, and C. M. Strong. 2000. Movement and territoriality of wintering hermit thrushes in Southeastern Louisiana. Wilson Bull. 112: 347-353.

Brown, L. H., E. K. Urban, K. Newman, M. Woodcock, and P. Hayman. 1982. The birds of Africa. Academic Press, London.

Broyer, J. 2009. Whinchat *Saxicola rubetra* reproductive success according to hay cutting schedule and meadow passerine density in alluvial and upland meadows in France. J. Nat. Conserv. 17: 160-167.

Bruderer, B., and A. Boldt. 2001. Flight characteristics of birds. Ibis 143: 178-204.

Bryant, D. M., and G. Jones. 1995. Morphological changes in a population of Sand Martins *Riparia riparia* associated with fluctuations in population size. Bird Study 42: 57-65.

Burfield, I. et al. 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge.

Butler, R. W., T. D. Williams, N. Warnock, and M. A. Bishop. 1997. Wind assistance: a requirement for migration of shorebirds? The Auk: 456-466.

Cade, B. S., and R. W. Hoffman. 1993. Differential Migration of Blue Grouse in Colorado. The Auk 110: 70-77.

Calladine, J., and J. Bray. 2012. The importance of altitude and aspect for breeding Whinchats *Saxicola rubetra* in the uplands: limitations of the uplands as a refuge for a declining, formerly widespread species? Bird Study 59: 43-51.

Callion, J. et al. 1993. Whinchat. Poyser, London.

Calvert, A. M., P. D. Taylor, and S. Walde. 2009. Cross-scale environmental influences on migratory stopover behaviour. Global Change Biol. 15: 744-759.

Calvert, A. M., J. Woodcock, and J. D. McCracken. 2010. Contrasting seasonal survivorship of two migratory songbirds wintering in threatened mangrove forests. Avian Conservation and Ecology 5: 2.

Cantos, F. J., and J. L. Tellería. 1994. Stopover site fidelity of four migrant warblers in the Iberian Peninsula. J. Avian Biol. 25: 131-134.

Carpenter, F. L., D. C. Paton, and M. A. Hixon. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proceedings of the National Academy of Sciences of the United States of America 80: 7259-7263.

Catry, I., P. Catry, T. Catry, and T. Martins. 2003. Within and between-year winter-site fidelity of Chiffchaffs *Phylloscopus collybita*. Ardea 91: 213-220.

Catry, I. et al. 2011. Individual variation in migratory movements and winter behaviour of Iberian Lesser Kestrels *Falco naumanni* revealed by geolocators. Ibis 153: 154-164.

Catry, P., S. Bearhop, and M. Lecoq. 2007. Sex differences in settlement behaviour and condition of chiffchaffs *Phylloscopus collybita* at a wintering site in Portugal. Are females doing better? J. Ornithol 148: 241-249.

Catry, P., A. Campos, V. Almada, and W. Cresswell. 2004a. Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. J. Avian Biol. 35: 204-209.

Catry, P. et al. 2004b. Are long-distance migrant passerines faithful to their stopover sites? J. Avian Biol. 35: 170-181.

Chandler, C. R., and R. S. Mulvihill. 1990. Interpreting differential timing of capture of sex classes during spring migration. J. Field Ornithol. 61: 85-89.

Chaplin, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 89: 321-330.

Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Influence of body condition on reproductive decision and reproductive success in the blue petrel. The Auk 112: 964-972.

Cheke, R. A., J. F. Venn, and P. J. Jones. 2007. Forecasting suitable breeding conditions for the red billed quelea *Quelea quelea* in southern Africa. J. Appl. Ecol. 44: 523-533.

Chernetsov, N. 1999. Timing of spring migration, body condition, and fat score in local and passage populations of the Reed Warbler *Acrocephalus scirpaceus* on the Courish Spit. Avian Ecology and Behaviour 2: 75-88.

Chernetsov, N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. J. Ornithol 147: 185-191.

Chernetsov, N. 2012a. Habitat selection and use by passerine migrants. Passerine migration: stopovers and flight. p 75-103. Springer Berlin Heidelberg.

Chernetsov, N. 2012b. Passerine migration: stopovers and flight. Springer Berlin Heidelberg.

Chernetsov, N., V. N. Bulyuk, and P. Ktitorov. 2007. Migratory stopovers of passerines in an oasis at the crossroads of the African and Indian flyways. Ringing Migr. 23: 243-251.

Chernetsov, N. S., E. A. Skutina, V. N. Bulyuk, and A. L. Tsvey. 2004. Optimal stopover decisions of migrating birds under variable stopover quality: model predictions and the field data. Zhurnal Obshche Biologii 65: 211-217.

Cimprich, D. A., M. S. Woodrey, and F. R. Moore. 2005. Passerine migrants respond to variation in predation risk during stopover. Anim. Behav. 69: 1173-1179.

Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). Mol. Ecol. 12: 819-830.

Coiffait, L., R. A. Robinson, J. A. Clark, and B. M. Griffin. 2011. Fattening strategies of British & Irish Barn Swallows *Hirundo rustica* prior to autumn migration. Ringing Migr. 26: 15-23.

Collier, P., G. Conway, and T. Venables. 2008. Climate change and Africa. Oxford Review of Economic Policy 24: 337-353.

Conklin, J. R., and P. F. Battley. 2012. Carry-over effects and compensation: late arrival on non-breeding grounds affects wing moult but not plumage or schedules of departing bar-tailed godwits *Limosa lapponica baueri*. J. Avian Biol. 43: 252-263.

Conway, C. J., G. V. N. Powell, and J. D. Nichols. 1995. Overwinter survival of Neotropical migratory birds in early-successional and mature tropical forests. Conserv. Biol. 9: 855-864.

Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy. 2013. Light-level geolocators reveal strong migratory connectivity and within-winter movements for a

coastal California Swainson's thrush (*Catharus ustulatus*) population. The Auk 130: 283-290.

Costantini, D., and A. P. Møller. 2013. A meta-analysis of the effects of geolocator application on birds. Current Zoology 59: 697-706.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences 100: 12219-12222.

Cowley, E. 1979. Sand Martin population trends in Britain, 1965–1978. Bird Study 26: 113-116.

Cowley, E., and G. M. Siriwardena. 2005. Long-term variation in survival rates of Sand Martins *Riparia riparia*: dependence on breeding and wintering ground weather, age and sex, and their population consequences. Bird Study 52: 237-251.

Cox, G. W. 1968. The role of competition in the evolution of migration. Evolution 22: 180-192.

Cramp, S. 1988. Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the western Palearctic. Vol. 5, Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Crawley, M. J. 2007. The R Book. John Wiley & Sons Ltd., Chichester.

Cresswell, W. 2009. The use of mass and fat reserve measurements from ringing studies to assess body condition. Ringing Migr. 24: 227-232.

Cresswell, W. 2014. Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis. Ibis 156: 493-510.

Cresswell, W., M. Boyd, and M. Stevens. 2009. Movements of Palearctic and Afrotropical bird species during the dry season (November–February) within Nigeria. In: D. M. Harebottle, A. J. F. K. Craig and M. D. Anderson, Rakotomanana, H. Muchai. (eds.) Proceedings of the 12th Pan African Ornithological Congress, 2008. p 8–28. Animal Demography Unit, Cape Town, South Africa.

Cresswell, W., J. M. Wilson, J. Vickery, P. Jones, and S. Holt. 2007. Changes in densities of Sahelian bird species in response to recent habitat degradation. Ostrich 78: 247-253.

Cuadrado, M. 1992. Year to year recurrence and site-fidelity of blackcaps *sylvia atricapilla* and robins erithacus rubecula in a mediterranean wintering area. Ringing Migr. 13: 36-42.

Cuadrado, M. 1995. Winter territoriality in migrant Black Redstarts *Phoenicurus ochrurus* in the Mediterranean area. Bird Study 42: 232-239.

Cuadrado, M. 1997. Why are migrant Robins (*Erithacus rubecula*) territorial in winter?: The importance of the anti-predatory behaviour. Ethol. Ecol. Evol. 9: 77-88.

Cuadrado, M., J. C. Senar, and J. L. Copete. 1995. Do all Blackcaps *Sylvia atricaplla* show winter site fidelity? Ibis 137: 70-75.

Curio, E. 1983. Why do young birds reproduce less well? Ibis 125: 400-404.

Currie, D., D. Thompson, and T. Burke. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. Ibis 142: 389-398.

Curry-Lindahl, K. 1981. Bird migration in Africa. Vol. 1. Academic Press, London.

Dänhardt, J., and Å. Lindström. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Anim. Behav. 62: 235-243.

Dauphiné, N., and R. J. Cooper. 2009. Impacts of free-ranging domestic cats (*Felis catus*) on birds in the United States: a review of recent research with conservation and management recommendations Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics No. 205. p 205-219. Partners In Flight, USA.

Davidson, N. C., and P. R. Evans. 1988. Prebreeding accumulation of fat and muscle protein by arctic-breeding shorebirds. In: H. Ouellet (ed.) Acta XIX Congressus Internationalis Ornithologici. p 342-352. University of Ottawa Press, Ottawa.

De La Hera, I., J. A. Diaz, J. Perez-Tris, and J. L. Telleria. 2009. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. J. Avian Biol. 40: 461-465.

DeGroote, L. W., and P. G. Rodewald. 2010. Blood parasites in migrating wood-warblers (*Parulidae*): effects on refueling, energetic condition, and migration timing. J. Avian Biol. 41: 147-153.

Dejaifve, P. A. 1994. Ecology and behavior of a palearctic migrant in Africa. The wintering of the winchat *Saxicola rubetra* in Zaïre and its winter distribution in Africa. Rev. Ecol. Terre. Vie. 49: 35-52.

Delingat, J., F. Bairlein, and A. Hedenström. 2007. Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). Behav. Ecol. Sociobiol. 62: 1069-1078.

Delingat, J., and V. Dierschke. 2000. Habitat utilization by Northern Wheatears (*Oenanthe oenanthe*) stopping over on an offshore island during migration. Vogelwarte 40: 271-278.

Delingat, J., V. Dierschke, H. Schmaljohann, and F. Bairlein. 2009. Diurnal patterns of body mass change during stopover in a migrating songbird, the Northern Wheatear *Oenanthe oenanthe*. J. Avian Biol. 40: 625-634.

Delingat, J., V. Dierschke, H. Schmaljohann, B. Mendel, and F. Bairlein. 2006. Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the Northern Wheatear *Oenanthe oenanthe*. Ardea 94: 593-605.

Delmore, K. E., J. W. Fox, and D. E. Irwin. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society B: Biological Sciences 279: 4582-4589.

Denlinger, D. L. 1980. Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. Biotropica 12: 100-106.

DeSante, D. F. 1983. Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. The Auk 100: 826-852.

Desante, D. F., K. M. Burton, J. F. Saracco, and B. L. Walker. 1995. Productivity indices and survival rate estimates from MAPS, a continent-wide programme of constant-effort mist-netting in North America. J. Appl. Statist. 22: 935-948.

Dierschke, V. 2003a. Predation hazard during migratory stopover: are light or heavy birds under risk? J. Avian Biol. 34: 24-29.

Dierschke, V. 2003b. Stopover behaviour of Northern Wheatears *Oenanthe oenanthe* on Helgoland: influence of foraging conditions during autumn migration. Vogelwelt 124: 165-176.

Dierschke, V., and J. Delingat. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behav. Ecol. Sociobiol. 50: 535-545.

Dierschke, V., B. Mendel, and H. Schmaljohann. 2005. Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? Behav. Ecol. Sociobiol. 57: 470-480.

Dierschke, V., H. Schmaljohann, and A. Walter. 2003. The role of predation risk in the stopover ecology of migrating passerines. Vogelwarte 42: 21-22.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, New York.

Drake, A., C. A. Rock, S. P. Quinlan, M. Martin, and D. J. Green. 2014. Wind speed during migration influences the survival, timing of breeding, and productivity of a neotropical migrant, *Setophaga petechia*. PLoS ONE 9: e97152.

Dugger, K. M., J. Faaborg, W. J. Arendt, and K. A. Hobson. 2004. Understanding survival and abundance of overwintering warblers: does rainfall matter? The Condor 106: 744-760.

Dunn, E. H. 2000. Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. The Auk 117: 12-21.

Dunn, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bull. 114: 368-379.

Duriez, O., B. J. Ens, R. Choquet, R. Pradel, and M. Klaassen. 2012. Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. Oikos 121: 862-873.

Egevang, C. et al. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. Proceedings of the National Academy of Sciences 107: 2078-2081.

Ekholm, A. 1982. Ringing of Bluethroats in Sandviken. Faglar i X-lan 14: 15-25.

Ekholm, A. 1988. Weight changes in resting Bluethroats. Faglar i X-lan 19: 14-26.

Ekstrom, P. A. 2004. An advance in geolocation by light. In: Y. Naito (ed.) Memoirs of the National Institue of Polar Research, Special Issue. p 210-226. National Institue of Polar Research, Tokyo.

Elgood, J. H., R. E. Sharland, and P. Ward. 1966. Palaearctic migrants in Nigeria. Ibis 108: 84-116.

Elkins, N. 2004. Weather and bird behaviour. 3rd ed. A & C Black, UK.

Ellegren, H. 1990. Autumn migration speed in Scandinavian Bluethroats *Luscinia s. svecica*. Ringing Migr. 11: 121-131.

Ellegren, H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. Ornis Scandinavica 22: 340-348.

Enstrom, D. A. 1992. Delayed plumage maturation in the orchard oriole (*Icterus spurius*): tests of winter adaptation hypotheses. Behav. Ecol. Sociobiol. 30: 35-42.

Eraud, C. et al. 2013. Migration routes and staging areas of trans-saharan Turtle Doves appraised from light-level geolocators. PLoS ONE 8: e59396.

Ergon, T., and B. Gardner. 2013. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture-recapture data. Methods Ecol. Evol.

Erni, B., F. Liechti, and B. Bruderer. 2002a. Stopover strategies in passerine bird migration: a simulation study. J. Theor. Biol. 219: 479-493.

Erni, B., F. Liechti, and B. Bruderer. 2005. The role of wind in passerine autumn migration between Europe and Africa. Behav. Ecol. 16: 732-740.

Erni, B., F. Liechti, L. G. Underhill, and B. Bruderer. 2002b. Wind and rain govern the intensity of nocturnal bird migration in central Europe: a log-linear regression analysis. Ardea 90: 155-166.

ERSI. 2012. ArcGIS Desktop: Release 10. California, Environmental Systems Research Institute, Redlands.

European Bird Census Council. 2012. Trends of common birds in Europe, 2012 update. http://www.ebcc.info/index.php?ID=485.

Farmer, A. H., and J. A. Wiens. 1999. Models and reality: time-energy trade-offs in pectoral sandpiper (*Calidris melanotos*) migration. Ecology 80: 2566-2580.

Fauchereau, N., S. Trzaska, M. Rouault, and Y. Richard. 2003. Rainfall variability and changes in Southern Africa during the 20th century in the global warming context. Nat. Hazards 29: 139-154.

Figuerola, J., and A. Bertolero. 1998. Sex differences in the stopover ecology of Curlew Sandpipers *Calidris ferruginea* at a refuelling area during autumn migration. Bird Study 45: 313-319.

Figuerola, J., R. Jovani, and D. Sol. 2001. Age-related habitat segregation by robins *Erithacus rubecula* during the winter. Bird Study 48: 252-255.

Finlayson, J. C. 1981. Seasonal distribution, weights and fat of passerine migrants at Gibraltar. Ibis 123: 88-95.

Fischer, K., R. Busch, G. Fahl, M. Kunz, and M. Knopf. 2012. Habitat preferences and breeding success of Whinchats (*Saxicola rubetra*) in the Westerwald mountain range. J. Ornithol 154: 339-349.

Flinks, H., B. Helm, and P. Rothery. 2008. Plasticity of moult and breeding schedules in migratory European Stonechats *Saxicola rubicola*. Ibis 150: 687-697.

Foppen, R., C. J. F. ter Braak, J. Verboom, and R. Reijnen. 1999. Dutch sedge warblers *Acrocephalus schoenobaenus* and West-African rainfall: empirical data and simulation modelling show low population resilience in fragmented marshlands. Ardea 87: 113-127.

Förschler, M. I., E. del Val, and F. Bairlein. 2010. Extraordinary high natal philopatry in a migratory passerine. J. Ornithol 151: 745-748.

Forstmeier, W. 2002. Benefits of early arrival at breeding grounds vary between males. J. Anim. Ecol. 71: 1-9.

Fox, A. D., C. M. Glahder, and A. J. Walsh. 2003. Spring migration routes and timing of Greenland white-fronted geese - results from satellite telemetry. Oikos 103: 415-425.

Fox, J., and H. S. Weisberg. 2010. An R companion to applied regression. Sage Publications, California.

Fox, J. W. 2010. Geolocator manual v8 (March 2010). http://www.antarctica.ac.uk/engineering/geo_downloads/Geolocator_manual_v8.pdf.

Francis, C. M., and F. Cooke. 1986. Differential timing of spring migration in Wood Warblers (*Parulinae*). The Auk 103: 548-556.

Fransson, T. 1995. Timing and speed of migration in North and West European populations of Sylvia warblers. J. Avian Biol. 26: 39-48.

Fransson, T. 1998. Patterns of migratory fuelling in Whitethroats *Sylvia communis* in relation to departure. J. Avian Biol. 29: 569-573.

Fransson, T., S. Jakobsson, and C. Kullberg. 2005. Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas. J. Avian Biol. 36: 6-11.

Fransson, T., and T. P. Weber. 1997. Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. Behav. Ecol. Sociobiol. 41: 75-80.

Fraser, K. C. et al. 2013. Consistent range-wide pattern in fall migration strategy of purple martin (*Progne subis*), despite different migration routes at the Gulf of Mexico. The Auk 130: 291-296.

Fraser, K. C. et al. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proceedings of the Royal Society B: Biological Sciences 279: 4901-4906.

Fry, C. H., J. S. Ash, and I. J. Ferguson Lees. 1970. Spring weights of some Palaearctic migrants at Lake Chad. Ibis 112: 58-82.

Fusani, L., M. Cardinale, C. Carere, and W. Goymann. 2009. Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines. Biol. Lett. 5: 302-305.

Garvin, M. C., C. C. Szell, and F. R. Moore. 2006. Blood parasites of Nearctic-Neotropical migrant passerine birds during spring trans-gulf migration: impact on host body condition. J. Parasitol. 92: 990-996.

Gauthreaux Jr, S. A. 1982. The ecology and evolution of avian migration systems. Avian biology 6: 93-168.

Gibbons, D. W., J. B. Reid, and R. A. Chapman. 1993. The new atlas of breeding birds in Britain and Ireland: 1988-1991. Poyser, London.

Gil, D., and P. J. B. Slater. 2000. Multiple song repertoire characteristics in the Willow Warbler (*Phylloscopus trochilus*): correlations with female choice and offspring viability. Behav. Ecol. Sociobiol. 47: 319-326.

Gill Jr, R. E., T. Piersma, G. Hufford, R. Servranckx, and A. Riegen. 2005. Crossing the ultimate ecological barrier: evidence for an 11 000-km-long nonstop flight

from Alaska to New Zealand and eastern Australia by bar-tailed godwits. The Condor 107: 1-20.

Gill Jr, R. E. et al. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proceedings of the Royal Society B: Biological Sciences 276: 447-457.

Gilroy, J. J., T. Virzi, R. L. Boulton, and J. L. Lockwood. 2012. A new approach to the "apparent survival" problem: estimating true survival rates from mark–recapture studies. Ecology 93: 1509-1516.

González-Prieto, A. M., and K. A. Hobson. 2013. Environmental conditions on wintering grounds and during migration influence spring nutritional condition and arrival phenology of Neotropical migrants at a northern stopover site. J. Ornithol 154: 1067-1078.

Google. 2012. Google Earth, version 6.2.

Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. Clim. Res. 35: 37-58.

Gordo, O., L. Brotons, X. Ferrer, and P. Comas. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans Saharan migrant birds? Global Change Biol. 11: 12-21.

Gordo, O., and J. J. Sanz. 2007. The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. J. Ornithol 149: 199-210.

Green, G. H., J. J. D. Greenwood, and C. S. Lloyd. 1977. The influence of snow conditions on the date of breeding of wading birds in north east Greenland. J. Zool. 183: 311-328.

Greenberg, R. 1986. Competition in migrant birds in the nonbreeding season. Current ornithology 3: 281-307.

Greenberg, R. 1992. Forest migrants in non-forest habitats on the Yucatan Peninsula. In: J. M. H. III and D. W. Johnston (eds.). p 273-286. Smithsonian Institution Press, Washington, D.C.

Greenberg, R., and P. P. Marra. 2005. Birds of two worlds: the ecology and evolution of migration. John Hopkins Univ Press, Baltimore.

Grüebler, M. U., F. Korner-Nievergelt, and B. Naef-Daenzer. 2014. Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. Ecology and Evolution 4: 756-765.

Grüebler, M. U. et al. 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. Biol. Conserv. 141: 3040-3049.

Gudmundsson, G. A., Å. Lindström, and T. Alerstam. 1991. Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. Ibis 133: 140-152.

Gunnarsson, T. G., J. A. Gill, J. Newton, P. M. Potts, and W. J. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 272: 2319-2323.

Gwinner, E. 1996. Circadian and circannual programmes in avian migration. J. Exp. Biol. 199: 39-48.

Hagemeijer, W. J. M., and M. J. Blair. 1997. The EBCC atlas of European breeding birds: their distribution and abundance. Poyser, London.

Hahn, T. P., J. Swingle, J. C. Wingfield, and M. Ramenofsky. 1992. Adjustments of the prebasic molt schedule in birds. Ornis Scandinavica 23: 314-321.

Hall, K. S. S., and T. Fransson. 2001. Wing moult in relation to autumn migration in adult Common Whitethroats *Sylvia communis communis*. Ibis 143: 580-586.

Handel, C. M., and R. E. Gill Jr. 2010. Wayward youth: Trans-Beringian movement and differential southward migration by juvenile sharp-tailed sandpipers. Arctic 63: 273-288.

Hanssen, S. A., D. Hasselquist, I. Folstad, and K. E. Erikstad. 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proceedings of the Royal Society B: Biological Sciences 272: 1039-1046.

Hansteen, T. L., H. P. Andreassen, and R. A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. J. Wildl. Manage. 61: 280-290.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology 79: 2376-2390.

Haukioja, E. 1971. Flightlessness in some moulting passerines in Northern Europe. Ornis Fenn. 48: 101-116.

Heckscher, C. M., S. M. Taylor, J. W. Fox, and V. Afanasyev. 2011. Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. The Auk 128: 531-542.

Hedenström, A. 1993. Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. Philosophical Transactions of the Royal Society B: Biological Sciences 342: 353-361.

Hedenström, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society B: Biological Sciences 363: 287-299.

Hedenström, A., and T. Alerstam. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. J. Theor. Biol. 189: 227-234.

Hedenström, A., and T. Alerstam. 1998. How fast can birds migrate? J. Avian Biol. 29: 424-432.

Hedenström, A., S. Bensch, D. Hasselquist, M. Lockwood, and U. Ottosson. 1993. Migration, stopover and moult of the great reed warbler *Acrocephalus arundinaceus* in Ghana, West Africa. Ibis 135: 177-180.

Hedenström, A., and J. Petterson. 1987. Migration routes and wintering areas of willow warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia. Ornis Fenn. 64: 137-143.

Heldbjerg, H., and T. Fox. 2008. Long-term population declines in Danish trans-Saharan migrant birds. Bird Study 55: 267-279.

Henderson, I. G., R. J. Fuller, G. J. Conway, and S. J. Gough. 2004. Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. Bird Study 51: 12-19.

Herremans, M. 1997. Habitat segregation of male and female Red-backed shrikes *Lanius collurio* and Lesser Grey Shrikes *Lanius minor* in the Kalahari basin, Botswana. J. Avian Biol. 28: 240-248.

Herremans, M., D. Herremans-Tonnoeyr, and W. D. Borello. 1995. Non-breeding site-fidelity of Red-backed Shrikes *Lanius collurio* in Botswana. Ostrich 66: 145-147.

Herzog, P. W., and D. M. Keppie. 1980. Migration in a local population of Spruce Grouse. The Condor 82: 366-372.

Hilgerloh, G., and W. Wiltschko. 2000. Autumn fat load and flight range of passerine long-distance migrants in southwestern Spain and northwestern Morocco. Ardeola 47: 259-263.

Hill, G. E. 1988. The function of delayed plumage maturation in male Black-Headed Grosbeaks. The Auk 105: 1-10.

Hill, R. D., and M. J. Braun. 2001. Geolocation by light level - the next step: Latitude. In: J. R. Sibert and J. L. Nielsen (eds.) Electronic tagging and tracking in marine fisheries. p 315-330. Kluwer Academic Publishers, Dordrecht.

Hobson, K. A., Y. Aubry, and L. I. Wassenaar. 2004. Migratory connectivity in Bicknell's Thrush: Locating missing populations with hydrogen isotopes. The Condor 106: 905-909.

Holmes, R. T. 2007. Understanding population change in migratory songbirds: long term and experimental studies of Neotropical migrants in breeding and wintering areas. Ibis 149: 2-13.

Holmes, R. T., and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation. In: I. J. M. Hagan and D. W. Johnston (eds.) Ecology and Conservation of Neotropical Migrant Landbirds. p 563-575. Smithsonian Institution Press., Washington D.C.

Holmes, R. T., T. W. Sherry, and L. Reitsma. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. The Condor 91: 545-561.

Horch, P., and S. Birrer. 2011. Cattle exclosure plots to enhance breeding whinchat *Saxicola rubetra* numbers on sub-alpine pasture at Bever, Graubünden Canton, Switzerland. Conservation Evidence 8: 81-86.

Houston, A. I. 1998. Models of optimal avian migration: state, time and predation. J. Avian Biol. 29: 395-404.

Houston, A. I., and J. M. McNamara. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. Ornis Scandinavica 24: 205-219.

Houston, A. I., N. J. Welton, and J. M. McNamara. 1997. Acquisition and maintenance costs in the long-term regulation of avian fat reserves. Oikos 78: 331-340.

Hulme, M. F., and W. Cresswell. 2012. Density and behaviour of Whinchats *Saxicola rubetra* on African farmland suggest that winter habitat conditions do not limit European breeding populations. Ibis 154: 680-692.

Hurly, T. A. 1992. Energetic reserves of marsh tits (*Parus palustris*): food and fat storage in response to variable food supply. Behav. Ecol. 3: 181-188.

Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. In: M. L. Cody (ed.) Habitat selection in birds. p 455-476. Academic Press, Orlando, FL.

Hutto, R. L. 1988. Is tropical deforestation responsible for the reported declines in neotropical migrant populations. American Birds 42: 375-379.

Hutto, R. L. 1992. Habitat distributions of migratory landbird species in western Mexico. In: I. J. M. Hagan and D. W. Johnston (eds.) Ecology and conservation of neotropical migrant landbirds. p 221-239. Smithsonian Institution Press, Washington, D.C.

Inger, R. et al. 2008. Habitat utilisation during staging affects body condition in a long distance migrant, *Branta bernicla hrota*: potential impacts on fitness? J. Avian Biol. 39: 704-708.

Inger, R. et al. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. J. Anim. Ecol. 79: 974-982.

Jahn, A. E. et al. 2013. Migration timing and wintering areas of three species of flycatchers (Tyrannus) breeding in the Great Plains of North America. The Auk 130: 247-257.

Jehl Jr, J. R. 1997. Cyclical changes in body composition in the annual cycle and migration of the Eared Grebe *Podiceps nigricollis*. J. Avian Biol. 28: 132-142.

Jenni, L., and M. Kéry. 2003. Timing of autumn bird migration under climate change: advances in long–distance migrants, delays in short–distance migrants. Proceedings of the Royal Society of London. Series B: Biological Sciences 270: 1467-1471.

Jenni, L., and R. Winkler. 2004. Moult and ageing of European passerines. Academic Press, London.

Jenni-Eiermann, S. et al. 2010. Numbers, foraging and refuelling of passerine migrants at a stopover site in the western Sahara: diverse strategies to cross a desert. J. Ornithol.

Jones, J. et al. 2008. Migratory connectivity and rate of population decline in a vulnerable songbird. The Condor 110: 538-544.

Jones, P., D. M. Newbery, H. H. T. Prins, and N. D. Brown. 1996a. Community dynamics of arboreal insectivorous birds in African savannas in relation to seasonal rainfall patterns and habitat change. In: D. M. Newberry, H. H. T. Prins and N. D. Brown (eds.) Dynamics of tropical communities. p 421-447. Blackwell Science, Oxford.

Jones, P., J. Vickery, S. Holt, and W. Cresswell. 1996b. A preliminary assessment of some factors influencing the density and distribution of palearctic passerine migrants wintering in the Sahel zone of West Africa. Bird Study 43: 73-84.

Jones, P. J. 1995. Migration strategies of Palearctic passerines in Africa. Isr. J. Zool. 41: 393-406.

Jones, T., and W. Cresswell. 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? J. Anim. Ecol. 79: 98-108.

Kaiser, H. F. 1958. The varimax criterion for analytic rotation in factor analysis. Psychometrika 23: 187-200.

Kalnay, E. et al. 1996. The NCEP/NCAR 40-year reanalysis project. Bulletin of the American meteorological Society 77: 437-471.

Kanyamibwa, S., A. Schierer, R. Pradel, and J. D. Lebreton. 1990. Changes in adult annual survival rates in a western European population of the White Stork *Ciconia ciconia*. Ibis 132: 27-35.

Karason, W. H., and B. Pinshow. 1998. Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiol. Zool. 71: 435-438.

Karlsson, H., C. Nilsson, J. Bäckman, and T. Alerstam. 2011. Nocturnal passerine migration without tailwind assistance. Ibis 153: 485-493.

Karlsson, H., C. Nilsson, J. Bäckman, and T. Alerstam. 2012. Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. Anim. Behav. 83: 87-93.

Karr, J. R. 1976. On the relative abundance of migrants from the north temperate zone in tropical habitats. Wilson Bull. 88: 433-458.

Keller, V., N. Zbinden, H. Schmid, and B. Volet. 2001. Rote Liste der gefährdeten Brutvogelarten der Schweiz. Vollzug Umwelt. Bundesamt für Umwelt, Wald und Landschaft, Bern, und Schweizerische Vogelwarte, Sempach.

Kelsey, M. G. 1989. A comparison of the song and territorial behaviour of a long-distance migrant, the Marsh Warbler *Acrocephalus palustris*, in summer and winter. Ibis 131: 403-414.

Kemp, M. U., J. Shamoun-Baranes, A. M. Dokter, E. van Loon, and W. Bouten. 2013. The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. Ibis 155: 734-749.

Kemp, M. U., J. Shamoun-Baranes, H. Van Gasteren, W. Bouten, and E. E. Van Loon. 2010. Can wind help explain seasonal differences in avian migration speed? J. Avian Biol. 41: 672-677.

Kemp, M. U. et al. 2012. Quantifying flow-assistance and implications for movement research. J. Theor. Biol. 308: 56-67.

Ketterson, E. D., and V. Nolan Jr. 1983. The evolution of differential bird migration. Current Ornithology 1: 357-402.

King, J. M. B., and J. M. C. Hutchinson. 2001. Site fidelity and recurrence of some migrant bird species in The Gambia. Ringing Migr. 20: 292-302.

Kirby, J. S. et al. 2008. Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conservation International 18: S49.

Kjellén, N. 1994. Moult in relation to migration in birds - a review. Ornis Svec. 4: 1-24.

Klaassen, M. 1996. Metabolic constraints on long-distance migration in birds. J. Exp. Biol. 199: 57-64.

Klaassen, R. H. G., T. Alerstam, P. Carlsson, J. W. Fox, and Å. Lindström. 2011. Great flights by great snipes: long and fast non-stop migration over benign habitats. Biol. Lett. 7: 833-835.

Klaassen, R. H. G., R. Strandberg, M. Hake, and T. Alerstam. 2008. Flexibility in daily travel routines causes regional variation in bird migration speed. Behav. Ecol. Sociobiol. 62: 1427-1432.

Koce, U., and D. Denac. 2010. Social foraging and habitat use by a long-distance passerine migrant, Whinchat *Saxicola rubetra*, at a spring stopover site on the SE Adriatic coast. J. Ornithol 151: 655-663.

Kok, O. B., C. A. Van Ee, and D. G. Nel. 1991. Daylength determines departure date of the spotted flycatcher *Muscicapa striata* from its wintering grounds. Ardea 79: 63-66.

Kokko, H. 1999. Competition for early arrival in migratory birds. J. Anim. Ecol. 68: 940-950.

Komenda-Zehnder, S., F. Liechti, and B. Bruderer. 2002. Is reverse migration a common feature of nocturnal bird migration? An analysis of radar data from Israel. Ardea 90: 325-334.

Koronkiewicz, T. J., M. K. Sogge, C. Van Riper III, and E. H. Paxton. 2006. Territoriality, site fidelity, and survivorship of Willow Flycatchers wintering in Costa Rica. The Condor 108: 558-570.

Kricher, J. C., and W. E. Davis, Jr. 1986. Returns and winter-site fidelity of North American migrants banded in Belize, Central America. J. Field Ornithol. 57: 48-52.

Kristensen, M. W., A. P. Tøttrup, and K. Thorup. 2013. Migration of the Common Redstart (*Phoenicurus phoenicurus*): a Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. The Auk 130: 258-264.

Kullberg, C., T. Fransson, and S. Jakobsson. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). Proceedings of the Royal Society B: Biological Sciences 263: 1671-1675.

Labhardt, A. 1988. Siedlungsstruktur von Braunkehlchen-Populationen auf zwei Höhenstufen der Westschweizer Voralpen. Beih Veröff Naturschutz Landschaftspflege Bad-Württ 51: 139-158.

Lack, D., and R. Gillmor. 1966. Population studies of birds. Clarendon Press, Oxford.

Lack, P. 1990. Palaearctic-African systems. In: A. Keast (ed.) Biogeography and ecology of forest bird communities. . p 345-356. SPB Academic Publishing, The Hague, Netherlands.

Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. Oikos 103: 303-319.

Latta, S. C., and J. Faaborg. 2001. Winter site fidelity of Prairie Warblers in the Dominican Republic. The Condor 103: 455-468.

Latta, S. C., and J. Faaborg. 2002. Demographic and population responses of Cape May Warblers wintering in multiple habitats. Ecology 83: 2502-2515.

Leisler, B. 1990. Selection and Use of Habitat of Wintering Migrants. In: E. Gwinner (ed.) Bird Migration. p 156-174. Springer Berlin Heidelberg.

Leisler, B. 1992. Habitat selection and coexistence of migrants and Afrotropical residents. Ibis 134: 77-82.

Lemke, H. W. et al. 2013. Annual cycle and migration strategies of a trans-Saharan migratory songbird: a geolocator study in the Great Reed Warbler. PLoS ONE 8: e79209.

Levey, D. J., and F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. The American Naturalist 140: 447-476.

Liechti, F. 2006. Birds: blowin' by the wind? J. Ornithol 147: 202-211.

Liechti, F., W. Witvliet, R. Weber, and E. Bachler. 2013. First evidence of a 200-day non-stop flight in a bird. Nature Communications 4: 2554.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67: 377-385.

Lind, J., and W. Cresswell. 2006. Anti-predation behaviour during bird migration; the benefit of studying multiple behavioural dimensions. J. Ornithol 147: 310-316.

Lind, J., T. Fransson, S. Jakobsson, and C. Kullberg. 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. Behav. Ecol. Sociobiol. 46: 65-70.

Lindström, Å. 1995. Stopover ecology of migrating birds: some unsolved questions. Isr. J. Zool. 41: 407-416.

Lindström, Å., and T. Alerstam. 1986. The adaptive significance of reoriented migration of Chaffinches *Fringilla coelebs* and Bramblings *F. montifringilla* during Autumn in Southern Sweden. Behav. Ecol. Sociobiol. 19: 417-424.

Lindström, Å., and D. Hasselquist. 1989. Why feed Bluethroats with mealworms? Roskarlen 11: 8-16.

Lindström, Å., D. Hasselquist, S. Bensch, and M. Grahn. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. Anim. Behav. 40: 453-461.

Lisovski, S., S. Bauer, T. Emmenegger, and M. S. Lisovski. 2012a. Package 'GeoLight'.

Lisovski, S., and S. Hahn. 2012. GeoLight - processing and analysing light-based geolocator data in R. Methods Ecol. Evol 3: 1055-1059.

Lisovski, S. et al. 2012b. Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol. Evol 3: 603-612.

Loss, S. R., T. Will, and P. P. Marra. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4: 1396.

Lövei, G. L. 1989. Passerine migration between the Palaearctic and Africa. Current Ornithology 6: 143-174.

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. J. Avian Biol. 27: 164-170.

Lundberg, A., and R. V. Alatalo. 2010. The pied flycatcher. A&C Black.

Lundberg, A., R. V. Alatalo, A. Carlson, and S. Ulfstrand. 1981. Biometry, habitat distribution and breeding success in the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scandinavica 12: 68-79.

Lynch, J. F. 1992. Distribution of overwintering Nearctic migrants in the Yucatan Peninsula, II: Use of native and human-modified vegetation. In: I. J. M. Hagan and D. W. Johnston (eds.) Ecology and conservation of neotropical migrant landbirds. p 178-196. Smithsonian Institution Press, Washington D.C.

Lynch, J. F., E. S. Morton, and M. E. Van der Voort. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). The Auk 102: 714-721.

Lyons, J. E., and S. M. Haig. 1995. Fat content and stopover ecology of spring migrant Semipalmated Sandpipers in South Carolina. Condor 97: 427-437.

Macdonald, C. A., H. G. Gilchrist, T. K. Kyser, J. W. Fox, and O. P. Love. 2012. Strong migratory connectivity in a declining Arctic passerine. Animal Migration 1: 23-30.

MacLean, S. F. 1969. Ecological determinants of species diversity of arctic sandpipers near Barrow, Alaska, University of California, Berkeley.

MacLeod, R., J. Clark, and W. Cresswell. 2008. The starvation–predation risk trade off, body mass and population status in the Common Starling *Sturnus vulgaris*. Ibis 150: 199-208.

Magnin, G. 1991. Hunting and persecution of migratory birds in the Mediterranean region. ICBP Birdlife Technical Publication Series 12: 63-75.

Maillet, D., and J. M. Weber. 2006. Performance-enhancing role of dietary fatty acids in a long-distance migrant shorebird: the semipalmated sandpiper. J. Exp. Biol. 209: 2686-2695.

Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. Behav. Ecol. 11: 299-308.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282: 1884-1886.

Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. The Auk 118: 92-104.

Marshall, M. R., D. R. Diefenbach, L. A. Wood, and R. J. Cooper. 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help. Anim. Biodivers. Conserv. 27: 59-72.

Marshall, M. R. et al. 2000. Estimating survival of Neotropical-Nearctic migratory birds: are they dead or just dispersed. In: R. Bonney, D. N.Pashley, R. J.Cooper and L. Niles (eds.) US Forest Service General Technical Report RMRS–P–16. U.S. Department of Agriculture Forest Service, Ogden, Utah.

Martin, G., and J. Busby. 1990. Birds by night. Poyser, London.

McCulloch, M. N., G. M. Tucker, and S. R. Baillie. 1992. The hunting of migratory birds in Europe: a ringing recovery analysis. Ibis 134: 55-65.

McKinnon, E. A., K. C. Fraser, C. Q. Stanley, and B. J. M. Stutchbury. 2014. Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. PloS one 9: e105605.

McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury. 2013a. New discoveries in landbird migration using geolocators, and a flight plan for the future. The Auk 130: 211-222.

McKinnon, E. A. et al. 2013b. Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. Animal Migration 1: 31-38.

McNamara, J. M., and A. I. Houston. 1990. The value of fat reserves and the tradeoff between starvation and predation. Acta Biotheoretica 38: 37-61.

McNeil, R. 1982. Winter resident repeats and returns of austral and boreal migrant birds banded in Venezuela. J. Field Ornithol. 53: 125-132.

Menzel, A. et al. 2006. European phenological response to climate change matches the warming pattern. Global Change Biol. 12: 1969-1976.

Merilä, J. 1997. Fat reserves and moult-migration overlap in goldcrests, *Regulus regulus* - a trade-off? Ann. Zool. Fenn. 34: 229-234.

Møller, A. P. 1990. Male tail length and female mate choice in the monogamous swallow *Hirundo rustica*. Anim. Behav. 39: 458-465.

Møller, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. Behav. Ecol. Sociobiol. 35: 115-122.

Møller, A. P. 2001. Heritability of arrival date in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 268: 203-206.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences of the United States of America 105: 16195-16200.

Møller, A. P., and T. Szép. 2005. Rapid evolutionary change in a secondary sexual character linked to climatic change. J. Evol. Biol. 18: 481-495.

Mönkkönen, M., R. Härdling, J. T. Forsman, and J. Tuomi. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. Evol. Ecol. 13: 93-106.

Moore, F., S. Mabey, and M. Woodrey. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. In: P. Berthold, E. Gwinner and E. Sonnenschein (eds.) Avian Migration. p 281-292. Springer Berlin Heidelberg.

Moore, F. R., and D. A. Aborn. 2000. Mechanisms of en route habitat selection: How do migrants make habitat decisions during stopover? Studies in Avian Biology 20: 34-42.

Moore, F. R. et al. 1995. Habitat requirements during migration: important link in conservation. In: T. E. Martin and D. M. Finch (eds.) Ecology and management of neotropical migratory birds, a synthesis and review of critical issues. . p 121-144. Oxford University Press, New York.

Moore, F. R., and W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. Behav. Ecol. Sociobiol. 28: 85-90.

Moreau, R. E. 1961. Problems of Mediterranean-Saharan migration. Ibis 103: 373-427.

Moreau, R. E. 1972. The Palaearctic-African bird migration systems. Academic Press, London.

Morganti, M. et al. 2011. Flexible tuning of departure decisions in response to weather in black redstarts *Phoenicurus ochruros* migrating across the Mediterranean Sea. J. Avian Biol. 42: 323-334.

Morris, S. R., M. E. Richmond, and D. W. Holmes. 1994. Patterns of stopover by warblers during spring and fall migration on Appledore Island, Maine. Wilson Bull. 106: 703-718.

Morton, E. S. 1990. Habitat segregation by sex in the hooded warbler: experiments on proximate causation and discussion of its evolution. Am. Nat. 135: 319-333.

Morton, E. S. 1992. What do we know about the future of migrant landbirds? In: J. M. Hagan and D. W. Johnston (eds.) Ecology and conservation of neotropical migrant landbirds. p 579-589. Smithsonian Institute Press, Washington, D.C.

Morton, E. S., J. F. Lynch, K. Young, and P. Mehlhop. 1987. Do male Hooded Warblers exclude females from nonbreeding territories in tropical forest? The Auk 104: 133-135.

Müller, M., R. Spaar, L. Schifferli, and L. Jenni. 2005. Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (*Saxicola rubetra*). J. Ornithol 146: 14-23.

Murray, B. G. 1979. Fall migration of blackpoll and yellow-rumped warblers at Island Beach, New Jersey. Bird-banding 50: 1-11.

Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Canadian Journal of Zoology 59: 1527-1534.

Newton, I. 2004. Population limitation in migrants. Ibis 146: 197-226.

Newton, I. 2006a. Advances in the study of irruptive migration. Ardea 94: 433-460.

Newton, I. 2006b. Can conditions experienced during migration limit the population levels of birds? J. Ornithol 147: 146-166.

Newton, I. 2007. Weather-related mass-mortality events in migrants. Ibis 149: 453-467.

Newton, I. 2010a. Bird migration. Collins, London, UK.

Newton, I. 2010b. The migration ecology of birds. Academic Press, London.

Nicholson, S. E., B. Some, and B. Kone. 2000. An analysis of recent rainfall conditions in West Africa, including the rainy seasons of the 1997 El Niño and the 1998 La Niña years. J. Clim. 13: 2628-2640.

Nilsson, C., R. H. G. Klaassen, and T. Alerstam. 2013. Differences in speed and duration of bird migration between spring and autumn. The American Naturalist 181: 837-845.

Nisbet, I. C. T., W. H. Drury Jr, and J. Baird. 1963. Weight-loss during migration Part I: Deposition and consumption of fat by the Blackpoll Warbler *Dendroica striata*. Bird Banding 34: 107-138.

Nisbet, I. C. T., and L. Medway. 1972. Dispersion, population ecology and migration of eastern great reed warblers *Acrocephalus orientalis* wintering in Malaysia. Ibis 114: 451-494.

Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. Oikos 109: 178-186.

Norris, D. R. et al. 2006. Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). Ornithological Monographs 61: 14-28.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 271: 59-64.

Norris, R. D., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. The Condor 109: 535-547.

Ockendon, N., C. M. Hewson, A. Johnston, and P. W. Atkinson. 2012. Declines in British-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. Bird Study 59: 111-125.

Ockendon, N., A. Johnston, and S. R. Baillie. 2014. Rainfall on wintering grounds affects population change in many species of Afro-Palaearctic migrants. J. Ornithol 155: 905-917.

Ockendon, N., D. Leech, and J. W. Pearce-Higgins. 2013. Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. Biol. Lett. 9: 20130669.

Odum, E. P., C. E. Connell, and H. L. Stoddard. 1961. Flight energy and estimated flight ranges of some migratory birds. The Auk 78: 515-527.

Oppermann, R. 1990. Suitability of different vegetation structure types as habitat for the whinchat (*Saxicola rubetra*). Vegetatio 90: 109-116.

Orlowski, G. 2004. Abandoned cropland as a habitat of the Whinchat *Saxicola rubetra* in SW Poland. Acta Ornithologica 39: 59-66.

Ornat, A. L., and R. Greenberg. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. The Auk 107: 539-543.

Otahal, C. D. 1995. Sexual Differences in Wilson's Warbler Migration. J. Field Ornithol. 66: 60-69.

Ottosson, U., J. Waldenstrom, C. Hjort, and R. McGregor. 2005. Garden Warbler *Sylvia borin* migration in sub-Saharan West Africa: phenology and body mass changes. Ibis 147: 750-757.

Parrish, J. D., and T. W. Sherry. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: importance of resource seasonality. The Auk 111: 38-49.

Peach, W. J., H. Q. P. Crick, and J. H. Marchant. 1995. The demography of the decline in the British willow warbler population. J. Appl. Statist. 22: 905-922.

Pearce-Higgins, J. W., and M. C. Grant. 2006. Relationships between bird abundance and the composition and structure of moorland vegetation: Capsule Variations in the composition, structure and heterogeneity of moorland vegetation are shown to affect the abundance of eight of nine moorland bird species, with implications for grazing management. Bird Study 53: 112-125.

Pearson, D. J. 1972. The wintering and migration of Palaearctic passerines at Kampala, southern Uganda. Ibis 114: 43-60.

Pearson, D. J. 1990. Palaearctic passerine migrants in Kenya and Uganda: temporal and spatial patterns of their movements. In: E. Gwinner (ed.) Bird Migration. p 44-59. Springer Berlin Heidelberg.

Pearson, D. J., and P. C. Lack. 1992. Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. Ibis 134: 89-98.

Pennycuick, C. J. 1972. Animal flight. Edward Arnold, London.

Pennycuick, C. J. 1975. Mechanics of flight. Avian biology 5: 1-75.

Pennycuick, C. J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press, Oxford, UK.

Pennycuick, C. J., and P. F. Battley. 2003. Burning the engine: a time-marching computation of fat and protein consumption in a 5420 km non-stop flight by great knots, *Calidris tenuirostris*. Oikos 103: 323-332.

Pérez-Tris, J., and J. L. Tellería. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. J. Anim. Ecol. 71: 211-224.

Petit, L. J., D. R. Petit, D. G. Christian, and H. D. W. Powell. 1999. Bird communities of natural and modified habitats in Panama. Ecography 22: 292-304.

Piersma, T., N. Cadée, and S. Daan. 1995. Seasonality in basal metabolic rate and thermal conductance in a long-distance migrant shorebird, the knot (*Calidris*

canutus). Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 165: 37-45.

Piersma, T., and S. van de Sant. 1992. Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. Ornis Svec. 2: 55-66.

Piper, W. H. 2011. Making habitat selection more "familiar": a review. Behav. Ecol. Sociobiol. 65: 1329-1351.

Porneluzi, P. A., and J. Faaborg. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. Conserv. Biol. 13: 1151-1161.

Potti, J. 1998. Arrival time from spring migration in male pied flycatchers: individual consistency and familial resemblance. Condor 100: 702-708.

Potti, J., and S. Montalvo. 1991. Male arrival and female mate choice in Pied Flycatchers *Ficedula hypoleuca* in Central Spain. Ornis scandinavica 22: 45-54.

Pulido, F. 2007. Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. Clim. Res. 35: 5-23.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rabøl, J. 1987. Coexistence and competition between overwintering Willow Warblers *Phylloscopus trochilus* and local warblers at Lake Naivasha, Kenya. Ornis Scandinavica 18: 101-121.

Ralph, C. J. 1978. Disorientation and possible fate of young passerine coastal migrants. Bird Banding 49: 237-247.

Ramenofsky, M., and J. C. Wingfield. 2006. Behavioral and physiological conflicts in migrants: the transition between migration and breeding. J. Ornithol 147: 135-145.

Rappole, J. H. 1995. The ecology migrant birds. A Neotropical perspective. Smithsonian Institution Press, Washington, D.C.

Rappole, J. H., D. I. King, and J. Diez. 2003. Winter vs. breeding-habitat limitation for an endangered avian migrant. Ecol. Appl. 13: 735-742.

Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. The Auk 111: 652-660.

Rappole, J. H., E. S. Morton, T. E. Lovejoy III, and J. R. Ruos. 1983. Nearctic avian migrants in the Neotropics. U.S. Fish and Wildlife Service, Washington, D.C.

Rappole, J. H., M. A. Ramos, and K. Winker. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. The Auk 106: 402-410.

Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. J. Field Ornithol. 62: 335-337.

Rappole, J. H., and D. W. Warner. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26: 193-212.

Remisiewicz, M., and L. Wennerberg. 2006. Differential migration strategies of the Wood Sandpiper (*Tringa glareola*) - genetic analyses reveal sex differences in morphology and spring migration phenology. Ornis Fenn. 83: 1-10.

Reudink, M. W. et al. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 276: 1619-1626.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Richardson, W. J. 1990. Timing of bird migration in relation to weather: updated review. In: E. Gwinner (ed.) Bird migration. p 78-101. Springer Berlin Heidelberg.

Risely, A., E. Blackburn, and W. Cresswell. 2014. Patterns in spring departure timing and mass gain on African wintering territories for a long distance migrant, the Whinchat (*Saxicola rubetra*). Manuscript submitted for publication.

Risely, K., Massimino, D., Johnston, A., Newson, S. E., Eaton, M. A., Musgrove, A. J., Noble, D. G., Procter, D. & Baillie, S. R. 2012. The Breeding Bird Survey 2011 BTO Research report No. 624. British Trust for Ornithology, Thetford.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences 86: 7658-7662.

Robertson, G. J., and F. Cooke. 1999. Winter philopatry in migratory waterfowl. The Auk 116: 20-34.

Robinson, R. A., D. E. Balmer, and J. H. Marchant. 2008. Survival rates of hirundines in relation to British and African rainfall. Ringing Migr. 24: 1-6.

Rockwell, S. M. 2013. Carry-over effects from the non-breeeding season influence spring arrival dates, reproductive success, and survival in an endangered migratory bird, the kirtland's warbler (*Setophaga kirtlandii*). Ph.D. thesis, University of Maryland.

Rubolini, D., A. Gardiazabal Pastor, A. Pilastro, and F. Spina. 2002. Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. J. Avian Biol. 33: 15-22.

Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark-recapture data. The Auk 128: 448-453.

Saino, N. et al. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society B: Biological Sciences 278: 835-842.

Saino, N. et al. 2007. Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. Clim. Res. 35: 123-134.

Saino, N. et al. 2009. Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. Biol. Lett. 5: 539-541.

Saino, N. et al. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecol. Lett. 7: 21-25.

Salewski, V. 2000. Microhabitat use and feeding strategies of the Pied Flycatcher and the Willow Warbler in their West-African winter quarters compared with resident species. Ostrich 71: 191-193.

Salewski, V., B. Almasi, A. Heuman, M. Thoma, and A. Schlageter. 2007. Agonistic behaviour of Palaearctic passerine migrants at a stopover site suggests interference competition. Ostrich 78: 349-355.

Salewski, V., F. Bairlein, and B. Leisler. 2000. Recurrence of some palaearctic migrant passerine species in West Africa. Ringing Migr. 20: 29-30.

Salewski, V., F. Bairlein, and B. Leisler. 2002a. Different wintering strategies of two Palearctic migrants in West Africa - a consequence of foraging strategies? Ibis 144: 85-93.

Salewski, V., F. Bairlein, and B. Leisler. 2003. Niche partitioning of two Palearctic passerine migrants with Afrotropical residents in their West African winter quarters. Behav. Ecol. 14: 493-502.

Salewski, V., K. H. Falk, F. Bairlein, and B. Leisler. 2002b. Numbers, body mass and fat scores of three Palearctic migrants at a constant effort mist netting site in Ivory Coast, West Africa. Ardea 90: 479-487.

Salewski, V., M. Herremans, and F. Liechti. 2010. Migrating passerines can lose more body mass that previously thought. Ringing Migr. 25: 22-25.

Salewski, V., and P. Jones. 2006. Palearctic passerines in Afrotropical environments: a review. J. Ornithol 147: 192-201.

Salewski, V., and M. Schaub. 2007. Stopover duration of Palearctic passerine migrants in the western Sahara - independent of fat stores? Ibis 149: 223-236.

Salewski, V., H. Schmaljohann, and F. Liechti. 2009. Spring passerine migrants stopping over in the Sahara are not fall-outs. J. Ornithol 151: 371-378.

Sandberg, R., and F. R. Moore. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. Oikos 77: 577-581.

Sanderson, F. J., P. F. Donald, D. J. Pain, I. J. Burfield, and F. P. J. Van Bommel. 2006. Long-term population declines in Afro-Palearctic migrant birds. Biol. Conserv. 131: 93-105.

Saurola, P. 1980. Recoveries of *Calidris* species ringed in Finland. Lintumies 15: 146-153. *Finnish with English summary*.

Sauvage, A., S. Rumsey, and S. Rodwell. 1998. Recurrence of Palaearctic birds in the lower Senegal river valley. Malimbus 20: 33-53.

Schäffer, N., B. A. Walther, K. Gutteridge, and C. Rahbek. 2006. The African migration and wintering grounds of the Aquatic Warbler *Acrocephalus paludicola*. Bird Conservation International 16: 33-56.

Schaub, M., and L. Jenni. 2000a. Body mass of six long-distance migrant passerine species along the autumn migration route. J. Ornithol 141: 441-460.

Schaub, M., and L. Jenni. 2000b. Fuel deposition of three passerine bird species along the migration route. Oecologia 122: 306-317.

Schaub, M., and L. Jenni. 2001. Variation of fuelling rates among sites, days and individuals in migrating passerine birds. Funct. Ecol. 15: 584-594.

Schaub, M., F. Liechti, and L. Jenni. 2004. Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. Anim. Behav. 67: 229-237.

Schaub, M. et al. 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. PLoS One 5: e13115.

Schaub, M., and J. A. Royle. 2013. Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. Methods Ecol. Evol: doi: 10.1111/2041-1210X.12134.

Schmaljohann, H. et al. 2011. Nocturnal exploratory flights, departure time, and direction in a migratory songbird. J. Ornithol 152: 439-452.

Schmaljohann, H., M. Buchmann, J. W. Fox, and F. Bairlein. 2012. Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. Behav. Ecol. Sociobiol. 66: 915-922.

Schmaljohann, H., F. Liechti, and B. Bruderer. 2007. Songbird migration across the Sahara: the non-stop hypothesis rejected! Proceedings of the Royal Society B: Biological Sciences 274: 735-739.

Schmidt, K., and E. Hantge. 1954. Studien an einer farbig beringten Population des Braunkehlchens (*Saxicola rubetra*). J. Ornithol 95: 130-173.

Schwartz, M. D., R. Ahas, and A. Aasa. 2006. Onset of spring starting earlier across the Northern Hemisphere. Global Change Biol. 12: 343-351.

Scott, I., P. I. Mitchell, and P. R. Evans. 1994. Seasonal changes in body mass, body composition and food requirements in wild migratory birds. Proceedings of the Nutrition Society 53: 521-531.

Senar, J. C., and N. B. Metcalfe. 1988. Differential use of local enhancement for finding food by resident and transient siskins. Anim. Behav. 36: 1549-1550.

Shannon, C. E. 2001. A mathematical theory of communication. ACM SIGMOBILE Mobile Computing and Communications Review 5: 3-55.

Sheehan, D. K., and F. J. Sanderson. 2012. Seeing the bigger picture: how anthropogenic landscape modification in Africa affects declining migratory

birds and the need for trans-continental research and conservation. Ibis 154: 659-662.

Sherry, T. W., and R. T. Holmes. 1993. Are populations of Neotropical migrant birds limited in summer or winter? Implications for management. In: D. M. Finch and P. W. Stangel (eds.) Status and management of Neotropical migratory birds. p 47-57. USDA Forest Service, General Technical Report RM-229., Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence. In: T. E. Martin and D. M. Finch (eds.) Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. p 85-120. Oxford University Press, New York.

Sherry, T. W., and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. Ecology 77: 36-48.

Sherry, T. W., M. D. Johnson, A. M. Strong, R. Greenberg, and P. P. Marra. 2005. Does winter food limit populations of migratory birds. In: R. Greenberg and P. P. Marra (eds.) Birds of two worlds: the ecology and evolution of migration. p 414-425. Johns Hopkins University Press, Baltimore, Maryland.

Shitikov, D. et al. 2012. Breeding-site fidelity and dispersal in isolated populations of three migratory passerines. Ornis Fenn. 89: 53-62.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. J. Anim. Ecol. 71: 296-308.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288: 2040-2042.

Sinclair, A. R. E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savannah. Ibis 120: 480-497.

Sinelschikova, A., V. Kosarev, I. Panov, and A. N. Baushev. 2007. The influence of wind conditions in Europe on the advance in timing of the spring migration of the song thrush (*Turdus philomelos*) in the south-east Baltic region. International Journal of Biometeorology 51: 431-440.

Skilleter, M. 1995. Winter site fidelity of Redstart *Phoenicurus phoenicurus* in N. Nigeria. Malimbus 17: 101-102.

Slagsvold, T., and J. T. Lifjeld. 1988. Plumage colour and sexual selection in the pied flycatcher *Ficedula hypoleuca*. Anim. Behav. 36: 395-407.

Smith, R. D., M. Marquiss, R. Rae, and N. B. Metcalfe. 1993. Age and sex variation in choice of wintering site by snow buntings: the effect of altitude. Ardea 81: 47-52.

Smith, R. J., S. E. Mabey, and F. R. Moore. 2009. Spring passage and arrival patterns of American Redstarts in Michigan's eastern upper peninsula. Wilson Journal of Ornithology 121: 290-297.

Smith, R. J., and F. R. Moore. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134: 325-331.

Smith, R. J., and F. R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behav. Ecol. Sociobiol. 57: 231-239.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68: 695-704.

Söderström, B., S. Kiema, and R. S. Reid. 2003. Intensified agricultural land-use and bird conservation in Burkina Faso. Agric., Ecosyst. Environ. 99: 113-124.

Sodhi, N. S., Ç. H. Şekercioğlu, J. Barlow, and S. K. Robinson. 2011. Conservation of tropical birds. Wiley-Blackwell, Oxford, UK.

Spina, F., A. Massi, and A. Montemaggiori. 1994. Back from Africa: who's running ahead? Aspects of differential migration of sex and age classes in Palearctic-African spring migrants. Ostrich 65: 137-150.

Spina, F., D. Piacentini, and A. Montemaggiori. 2006. Bird migration across the Mediterranean: ringing activities on Capri within the Progetto Piccole Isole. Ornis Svec. 16: 20-26.

Stach, R., S. Jakobsson, C. Kullberg, and T. Fransson. 2012. Geolocators reveal three consecutive wintering areas in the Thrush Nightingale. Animal Migration 1: 1-7.

Steifetten, Ø., and S. Dale. 2006. Viability of an endangered population of ortolan buntings: the effect of a skewed operational sex ratio. Biol. Conserv. 132: 88-97.

Stevens, M., D. Sheehan, J. Wilson, G. Buchanan, and W. Cresswell. 2010. Changes in Sahelian bird biodiversity and tree density over a five-year period in northern Nigeria. Bird Study 57: 156-174.

Stiles, F. G. 1980. Evolutionary implications of habitat relations between permanent and winter resident landbirds in Costa Rica. In: A. Keast and E. S. Morton (eds.) Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. p 421-435. Smithsonian Institution Press, Washington, D.C.

Stoate, C., and S. J. Moreby. 1995. Premigratory diet of trans-Saharan migrant passerines in the western Sahel. Bird Study 42: 101-106.

Strandberg, R., and T. Alerstam. 2007. The strategy of fly-and-forage migration, illustrated for the osprey (*Pandion haliaetus*). Behav. Ecol. Sociobiol. 61: 1865-1875.

Strandberg, R., R. H. G. Klaassen, M. Hake, and T. Alerstam. 2009. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. Biol. Lett. 10: 297-300.

Strong, A. M., and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. J. Anim. Ecol. 69: 883-895.

Studds, C. E., T. K. Kyser, and P. P. Marra. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. Proc. Natl. Acad. Sci. 105: 2929–2933.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86: 2380-2385.

Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Clim. Res. 35: 115-122.

Stutchbury, B. J. 1994. Competition for winter territories in a Neotropical migrant: the role of age, sex and color. The Auk 111: 63-69.

Sutherland, W. J. 1998. Evidence for flexibility and constraint in migration systems. J. Avian Biol. 29: 441-446.

Svensson, E., and A. Hedenström. 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: *Sylviidae*). Biol. J. Linn. Soc. 67: 263-276.

Swaddle, J. P., and M. S. Witter. 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. Canadian Journal of Zoology 75: 1135-1146.

Swaddle, J. P., M. S. Witter, I. C. Cuthill, A. Budden, and P. McCowen. 1996. Plumage condition affects flight performance in common starlings: implications for developmental homeostasis, abrasion and moult. J. Avian Biol. 27: 103-111.

Swanson, D. L., E. T. Liknes, and K. L. Dean. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant ruby-crowned kinglets. Wilson Bull. 111: 61-69.

Szep, T. 1995a. Relationship between west African rainfall and the survival of central European Sand Martins *Riparia riparia*. Ibis 137: 162-168.

Szep, T. 1995b. Survival rates of Hungarian sand martins and their relationship with Sahel rainfall. J. Appl. Statist. 22: 891-904.

Terrill, S. B. 1990. Ecophysiological aspects of movements by migrants in the wintering quarters. In: E. Gwinner (ed.) Bird migration. p 130-143. Springer Berlin Heidelberg.

Thaxter, C. B., A. C. Joys, R. D. Gregory, S. R. Baillie, and D. G. Noble. 2010. Hypotheses to explain patterns of population change among breeding bird species in England. Biol. Conserv. 143: 2006-2019.

Thompson, M. C. 1974. Migratory patterns of ruddy turnstones in the central Pacific region. Living Bird 12: 5-23.

Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky. 2002. Agricultural sustainability and intensive production practices. Nature 418: 671-677.

Tilman, D. et al. 2001. Forecasting agriculturally driven global environmental change. Science 292: 281-284.

Tome, D., and D. Denac. 2012. Survival and development of predator avoidance in the post-fledging period of the Whinchat (*Saxicola rubetra*): consequences for conservation measures. J. Ornithol 153: 131-138.

Tøttrup, A. P. et al. 2012. The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. Proceedings of the Royal Society B: Biological Sciences 279: 1008-1016.

Tøttrup, A. P. et al. 2008. Avian migrants adjust migration in response to environmental conditions en route. Biol. Lett. 4: 685-688.

Tryjanowski, P., A. Goławski, S. Kuźniak, T. Mokwa, and M. Antczak. 2007. Disperse or stay? Exceptionally High breeding-site infidelity in the Red-Backed Shrike *Lanius collurio*. Ardea 95: 316-320.

Tryjanowski, P., and R. Yosef. 2002. Differences between the spring and autumn migration of the Red-Backed Shrike *Lanius collurio*: record from the Eilat stopover (Israel). Acta Ornithologica 37: 85-90.

Tsvey, A., V. N. Bulyuk, and V. Kosarev. 2007. Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behav. Ecol. Sociobiol. 61: 1665-1674.

Tucker, G. M., M. F. Heath, L. Tomialojc, R. F. A. Grimmett, and C. M. Socha. 1994. Birds in Europe: their conservation status. BirdLife International, Cambridge.

Tucker, V. A. 1974. Energetics of natural avian flight. In: R. A. Paynter Jr (ed.) Avian energetics. p 298-333. Nutall Ornithological Club Publication, No.15, Cambridge, Massachusetts.

Underhill, L. G. et al. 1992. The biannual primary moult of Willow Warblers *Phylloscopus trochilus* in Europe and Africa. Ibis 134: 286-297.

Urquhart, E. 2002. Stonechats: a guide to the genus *Saxicola*. A&C Black.

Veiga, J. P. 1986. Settlement and fat accumulation by migrant Pied Flycatchers in Spain. Ringing Migr. 7: 85-98.

Verboven, N., and M. E. Visser. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. Oikos 81: 511-524.

Viallefont, A., F. Cooke, and J.-D. Lebreton. 1995. Age-specific costs of first-time breeding. The Auk 112: 67-76.

Vickery, J. A. et al. 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156: 1-22.

Visser, M. E., A. J. Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society B: Biological Sciences 265: 1867-1870.

Visser, M. E., A. C. Perdeck, J. H. Van Balen, and C. Both. 2009. Climate change leads to decreasing bird migration distances. Global Change Biol. 15: 1859-1865.

Waide, R. B. 1980. Resource partitioning between migrant and resident birds: the use of irregular resources. In: A. Keast and E. S. Morton (eds.) Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. p 337-352. Smithsonian Institution Press, Washington, D.C.

Waldenstrom, J., and U. Ottosson. 2002. Moult strategies in the common whitethroat *Sylvia c. communis* in northern Nigeria. Ibis 144: E11-E18.

Warkentin, I. G., and D. Hernandez. 1996. The conservation implications of site fidelity: a case study involving nearctic-neotropical migrant songbirds wintering in a Costa Rican mangrove. Biol. Conserv. 77: 143-150.

Warnock, N., and M. A. Bishop. 1998. Spring stopover ecology of migrant Western Sandpipers. Condor 100: 456-467.

Weber, T. P., J. Borgudd, A. Hedenström, K. Persson, and G. Sandberg. 2005. Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. Biol. Lett. 1: 27-30.

Weber, T. P., S. Kranenbarg, A. Hedenström, J. H. Waarsing, and H. Weinans. 2010. Flight feather shaft structure of two warbler species with different moult schedules: a study using high-resolution X-ray imaging. J. Zool. 280: 163-170.

Webster, M. S., P. P. Marra, R. Greenberg, and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. In: R. Greenberg and P. P. Marra (eds.) Birds of two worlds: the ecology and evolution of migration. p 199-209. Johns Hopkins University Press, Baltimore, Maryland.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends Ecol. Evol. 17: 76-83.

Wernham, C. 2002. The Migration Atlas: Movements of the Birds of Britain and Ireland. T. & A. D. Poyser Ltd, London.

Wiggins, D. A., T. Pärt, and L. Gustafsson. 1994a. Correlates of clutch desertion by female collared flycatchers *Ficedula albicollis*. J. Avian Biol. 25: 93-97.

Wiggins, D. A., T. Pärt, and L. Gustafsson. 1994b. Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. Oikos 70: 359-364.

Wilson, J., and W. Cresswell. 2010a. The Northern Wheatear *Oenanthe oenanthe* in the Sahel of West Africa: distribution, seasonal variation in abundance and habitat associations. Ostrich 81: 115-121.

Wilson, J. M., and W. Cresswell. 2006. How robust are Palearctic migrants to habitat loss and degradation in the Sahel? Ibis 148: 789-800.

Wilson, J. M., and W. Cresswell. 2010b. Densities of Palearctic warblers and Afrotropical species within the same guild in Sahelian West Africa. Ostrich 81: 225-232.

Winker, K. 1998. The concept of floater. Ornitol Neotropical 9: 111-119.

Winstanley, D., R. Spencer, and K. Williamson. 1974. Where have all the whitethroats gone? Bird Study 21: 1-14.

Wisz, M. S., B. A. Walther, and C. Rahbek. 2007. Using potential distributions to explore determinants of Western Palaearctic migratory songbird species richness in sub-Saharan Africa. J. Biogeogr. 34: 828-841.

Witter, M. S., and I. C. Cuthill. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society B: Biological Sciences 340: 73-92.

Wood, B. 1982. The trans-Saharan spring migration of yellow wagtails (*Motacilla flava*). J. Zool. 197: 267-283.

Wood, B. 1992. Yellow Wagtail *Motacilla flava* migration from West Africa to Europe: pointers towards a conservation strategy for migrants on passage. Ibis 134: 66-76.

Woodrey, M. S., D. Demarest, and E. R. Inzunza. 2005. Addressing conservation needs of birds during the migratory period: problems and approaches. In: C. J. Ralph and T. D. Rich (eds.) Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference Volume 2. General Technical Report PSW-GTR-191 No. 2. p 653-656, Albany, California: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.

Woodrey, M. S., and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. The Auk 114: 695-707.

Wunderle Jr, J. M. 1995. Population characteristics of Black-throated Blue Warblers wintering in three sites on Puerto Rico. The Auk 112: 931-946.

Wunderle Jr, J. M., and S. C. Latta. 2000. Winter site fidelity of Nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. The Auk 117: 596-614.

Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith, and J. Ireland. 2004. Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. Proceedings of the Royal Society B: Biological Sciences 271: 1263-1269.

Yeatman-Berthelot, D., G. Jarry, and M. Cambrony. 1995. Nouvel atlas des oiseaux nicheurs de France 1985-1989. Société ornithologique de France, Paris.

Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behav. Ecol. 15: 469-476.

Yohannes, E., H. Biebach, G. Nikolaus, and D. J. Pearson. 2008. Passerine migration strategies and body mass variation along geographic sectors across East Africa, the Middle East and the Arabian Peninsula. J. Ornithol 150: 369-381.

Yohannes, E., H. Biebach, G. Nikolaus, and D. J. Pearson. 2009. Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. J. Avian Biol. 40: 126-134.

Yohannes, E., K. A. Hobson, and D. J. Pearson. 2007. Feather stable-isotope profiles reveal stopover habitat selection and site fidelity in nine migratory species moving through sub-Saharan Africa. J. Avian Biol. 38: 347-355.

Yom-Tov, Y. 1984. On the difference between the spring and autumn migrations in Eilat, southern Israel. Ringing Migr. 5: 141-144.

Yunick, R. P. 1988. Differential spring migration of Dark-Eyed Juncos. J. Field Ornithol. 59: 314-320.

Zduniak, P., R. Yosef, and P. Tryjanowski. 2009. Effect of flooding on palearctic migrant birds at the Eilat stopover site in Israel. Ekologia Bratislava 28: 291-299.

APPENDIX

Figure A.1. Examples of study sites, showing typical conditions at the beginning (images A and B) and end (images C and D) of the wintering season. Note the decrease in ground vegetation from grazing and dryer conditions as the winter progresses.

Table A.1. Summary of all aspects of migration (±1 SE) for all geolocators retrieved for Chapter 6: *Migration*. In column '*n*' (sample size), '*birds'* is the number of individuals, whereas '*cases*' is the number of instances across all migratory traces.

Aspect of migration	Average (± SE)	95% CI	Std. dev	Range	*n*	
					birds	*cases*
Spring migration						
Last day on winter territory	105 (±2.3)	4.9	8.8	87 - 118	15	15
Last day south of Sahara	110 (±1.6)	3.5	6.4	99 - 121	15	15
Distance to breeding grounds (km)						
winter sun elevation angle	5947 (±204.7)	456.1	678.9	5026 - 7516	11	11
summer sun elevation angle	6223 (±190.0)	429.7	600.7	5597 - 7676	10	10
Total migration time (days)	20 (±2.2)	4.8	7.1	10 - 32	11	11
Total days actively migrating	10 (±0.4)	1.0	1.5	7 - 12	11	11
Average travel between stops (days)	4 (±0.4)	0.8	1.5	1 - 6	11	40
Average distance between stops (km)						
winter sun elevation angle	2241 (±161.7)	349.2	604.9	1282 - 3043	14	40
summer sun elevation angle	2308 (±172.4)	377.6	624.7	1307 - 3131	13	32
Average daily distance travelled (km)						
winter sun elevation angle	656 (±34.5)	74.6	129.1	447 – 880	14	39
summer sun elevation angle	715 (±44.1)	126.7	96.0	536 - 1072	13	31
Average minimum flight speed (km/hr)						
winter sun elevation angle	27.4 (±1.8)	3.0	5.2	19 - 37	14	39
summer sun elevation angle	29.7 (±1.8)	4.0	6.5	22 - 45	13	31
Number of stopovers	2 (±0.3)	0.7	1.0	1 - 4	11	11
Average stopover duration (days)	7 (±0.8)	1.7	3.1	2 - 13	15	28
Total days at stopovers	12 (±2.2)	4.9	7.3	2 - 24	11	11
Breeding						
Arrival at breeding grounds	125 (±2.0)	4.5	6.7	114 - 139	11	11
Days on breeding grounds	105 (±3.0)	7.0	8.4	92 - 116	8	8
Departure from breeding grounds	232 (±3.1)	7.4	8.9	220 - 248	8	8
Autumn migration						
Total migration time (days)	44 (±3.8)	9.0	10.7	35 - 86	8	8
Total days actively migrating	10 (±1.3)	3.0	3.6	5 - 17	8	8
Average travel between stops (days)	2 (±0.2)	0.5	0.6	1 - 3	8	42
Average distance between stops (km)						
winter sun elevation angle	850 (±89.6)	211.8	253.3	484 - 1280	8	17
summer sun elevation angle	775 (±105.3)	249.0	297.8	409 - 1245	8	17
Average daily distance travelled (km)						
winter sun elevation angle	510 (±51.8)	122.5	146.5	297 - 742	8	17
summer sun elevation angle	467 (±53.6)	126.7	151.5	238 - 705	8	17
Average minimum flight speed (km/hr)						
winter sun elevation angle	21 (±2.2)	5.2	6.2	12 - 31	8	17
summer sun elevation angle	20 (±2.2)	5.1	6.1	10 - 29	8	17
Number of stopovers	4 (±0.3)	0.7	1.0	3 - 5	9	9
Average stopover duration	10 (1.2)	2.7	3.5	4 - 13	9	34
Total days at stopovers	35 (±4.4)	10.2	13.2	13 - 63	9	9
Arrival on wintering grounds	277 (±3.5)	7.9	11.0	263 - 296	10	10